

Spotted Owl Food Habits and Prey

This appendix summarizes spotted owl¹ food habits and the habitat affinities of their major prey species. It also considers the possibilities for deliberately manipulating the owl's prey base through silvicultural prescriptions.

Owl Diets

Information on the composition of spotted owl diets over the bird's range from British Columbia to southern California (table J1), for both the northern and California subspecies, was gleaned from published and unpublished sources representing over 15,100 individual prey items examined in regurgitated owl pellets. For broad comparison, diets are presented as the percentage of individual prey identified in each sample of pellets. Species were sometimes lumped into generic or broader categories (for example, woodrats, voles, lagomorphs) to facilitate comparisons.

Although spotted owls eat a wide variety of prey, small mammals—particularly nocturnal arboreal or semi-arboreal species—predominate in diets when composition is expressed in either numbers or biomass consumed. Samples from individual studies often show that 70 to 90% of the prey biomass is contributed by just two or three species, particularly northern flying squirrels, dusky-footed or bushy-tailed woodrats, and various lagomorphs (hares and rabbits). Additionally, pocket gophers, red tree voles, and deer mice are regionally important. Flying squirrels are especially important in mesic forests of the Western Hemlock/Douglas-Fir Zones; woodrats often predominate in samples from drier mixed-conifer/mixed-evergreen forests. These trends are reflected in broad geographic differences in owl diets: flying squirrels tend to predominate from British Columbia to central Oregon, and woodrats predominate from southern Oregon through southern California. California and Oregon studies suggest that elevational differences in owl diets mirror latitudinal changes, with flying squirrels more abundant at higher elevations (particularly in true fir associations) and woodrats at lower elevations (Barrows 1980, Forsman et al. 1984, Neal et al. 1989, Paton et al. 1990).

Additional studies also support these interpretations. Forsman et al. (1989) report that flying squirrels were important owl prey on the Olympic Peninsula of Washington State. Bushy-tailed woodrats and western red-backed voles were important on the drier east side of the Peninsula, but not in west side rain forests. They also report that owl diets from the Roseburg, Oregon, area were dominated by woodrats in xeric mixed-evergreen forest types and by flying squirrels in more humid Douglas-fir types. Beebe and Schonewald (1977) note that owls in Main County, California, consumed woodrats and deer mice.

¹ Scientific names of mammals and birds are listed in appendix V, table V1.

Table J1—Food habits of the spotted owl in different regions (data represent percentage of prey numbers)

Region	Washington						Oregon				
Area	British Columbia	Cascades West		Cascades East		Olympic Peninsula	Coast Range				
Source	1	2	3	4	3	3	5	6	6	7	5
Vegetation	1	1	1	2	2	1	1	1	3	4	3
Sample size ^a	16	143	679	314	179	188	1214	194	298	52	566
Flying squirrel	31.2	12.6	27.1	36.0	46.9	45.7	35.2	30.9	15.8	40.4	13.8
Wood rats	—	—	0.7	8.0	0.6	5.3	4.9	11.9	25.2	7.7	4.9
Red tree vole	—	2.8	0	—	0	0	19.1	18.0	27.5	26.9	38.2
Other voles	—	42.7	16.2	5.0	5.0	4.3	6.2	6.2	7.0	0	1.6
Deer mouse	31.2	23.8	14.1	8.0	6.1	7.5	11.7	9.8	5.7	3.9	22.1
Lagomorphs	—	—	3.1	5.0	4.5	9.0	4.3	4.6	4.7	3.9	0.7
Other mammals	31.2	9.8	29.2	32.0	33.5	20.2	7.5	9.8	6.0	3.8	6.9
Birds	6.2	2.1	5.9	6.0	2.2	7.4	3.0	6.2	2.7	7.7	7.9
Other ^b	0.3	6.3	3.6	—	1.1	0.5	8.1	2.6	5.0	5.8	3.9

Table J1—continued

Region	Oregon(continued)								California					
Area	Cascades West			Cascades East		Southern (KlamathProvince)			Northwest					
Source	5	6	8	5	5	5	6	6	9	10	11	7	12	18
Vegetation	1	1	1	1	5	4	4	3	6	6	6	6	6	8
Sample size ^a	817	1062	364	191	555	651	187	530	240	375	1677	1356	495	75
Flying squirrel	42.4	35.2	43.1	12.0	25.1	17.7	19.3	29.5	7.1	14.9	13.8	22.5	12.7	12.8
Woodrats	2.2	11.4	8.0	1.6	7.0	39.0	29.3	13.0	45.0	29.9	18.0	31.4	36.3	38.5
Red tree vole	13.3	11.3	6.6	3.7	—	4.9	17.6	13.3	12.5	17.1	28.8	5.5	8.9	5.1
Other voles	11.2	11.3	15.4	14.7	5.4	15.6	10.2	13.6	6.2	—	3.6	11.9	11.8	3.9
Deer mouse	8.7	6.3	3.8	2.6	8.5	5.0	2.1	7.0	6.2	12.8	16.5	6.6	7.1	16.7
Lagomorphs	2.5	7.9	5.8	2.1	5.4	2.6	8.0	2.8	0.4	0.3	0.5	3.2	3.6	11.5
Other mammals	13.1	10.7	12.1	27.2	16.9	7.1	5.9	7.9	14.1	3.2	2.3	7.7	7.8	6.5
Birds	3.1	3.7	4.4	3.1	5.8	6.4	2.7	7.0	1.7	10.3	5.6	5.2	4.4	5.1
Other ^b	3.5	2.2	—	33.0	25.9	1.7	4.3	5.8	6.8	12.0	11.3	6.0	7.7	0

Footnotes at end of table.

Table J1—Continued

Region	California							
	Sierra Nevada ^c				Southern ^c			
Area								
Source	13	14	15	16	17	17	10	11
Vegetation	4	4	4	4	4	7	4	4
Sample size ^a	162	33	139	1275	1069	73	296	152
Flying squirrel	37.9	292	30.2	17.7	16.8	—	—	—
Woodrats	1.2	—	19.4	13.6	0.8	72.6	33.1	36.8
Red tree vole	—	—	—	—	—	—	—	—
Other voles	—	4.0	—	2.8	1.5	1.4	—	—
Deer mouse	6.5	9.1	8.6	15.4	9.6	9.6	30.7	32.9
Lagomorphs	—	—	—	—	—	—	0.3	0.7
Other mammals	20.2	24.3	17.9	18.0	21.9	9.6	9.4	11.9
Birds	4.2	18.2	13.9	16.9	14.9	1.4	9.2	6.5
Other ^b	30.0	15.1	10.0	15.3	34.4	5.5	17.6	11.2

^a Number of prey items.^b Insects, reptiles, arthropods, unknown.^c California spotted owl.

Source: (1) Smith 1963; (2) Hays, pets. comm.; (3) WDW 1990; (4) Richards 1989; (5) Forsman et. al. 1984; (6) Miller 1989; (7) Paton et. al. 1990, Ogan and Sakai 1990; (6) Meslow et al. 1989; (9) Solis 1983, (10) Barrows 1980; (11) Barrows 1987; (12) Ward and Gutiérrez 1989; (13) Roberts 1989, pers. comm.; (14) Marshall 1942; (15) Thrailkill and Bias 1990; (16) Laymon 1988; (17) Neal et. al. 1989, (18) Kerns 1989.

Vegetation: (1) western hemlock/Douglas-fir, (2) Douglas-fir, (3) valley edge/Douglas-fir/oak, (5) mixed conifer/evergreen, (5) Douglas-fir/ponderosa pine, (6) Douglas-fir/mixed evergreen, (7) oak woodland, (8) redwood/Douglas-fir.

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Forsman et al. (1989) describe seasonal shifts in dietary composition. Shifts seemed related to changes in seasonal abundance or vulnerability of particular prey: for example, above-ground periods of dispersal for pocket gophers and moles, presence of juvenile rabbits or hares of tractable size, and dispersal of juvenile flying squirrels from nests. No differences were detected in prey items for male and female owls. Laymon (1988) reported large pair-to-pair differences in the frequency of prey type from year to year and from site to site for 14 owl pairs in the central Sierra Nevada.

Studies of spotted owl diets suggest that understanding the ecology of comparatively few small mammal species—namely flying squirrels, woodrats, lagomorphs, and several voles—will contribute substantially to understanding the ecology of the owl.

Prey Abundance and Owl Reproduction

The relation of the reproductive success of spotted owls to the abundance of their principal prey also deserves comment. Based on studies of other owl species (see Ward and Gutiérrez 1989, for summary), spotted owl reproductive success could be more variable, or lower, wherever their principal prey fluctuate greatly in abundance, or are comparatively scarce or small. Southern's (1970) classic study of the tawny owl for example, showed that reproductive success was closely linked to prey numbers and availability. Tawny owls did not attempt to breed when rodent densities were low. Similarly, reproduction of great horned owls in Alberta seems closely tied to the abundance of prey, particularly snowshoe hares (Rusch et al. 1972).

The relation of prey abundance to reproductive success has not been well established for spotted owls. Ward and Gutiérrez (1989) were unable to demonstrate differences in prey abundance between reproducing and nonreproducing owl pairs by sampling prey at foraging sites used by the males. They suggest that this may have been due to the great variability in prey abundance encountered within owl home ranges, and also the low power of the statistical tests used in comparisons. Barrows (1985, 1987), however, reported that successful reproduction for spotted owls in California seemed correlated with the occurrence of large prey (100 g or larger) in owl diets. He recognized that the frequency of large prey in diets was a complex function of its availability and selection by owls. Recently, Laymon (1988) and Thrailkill and Bias (1990) report similar positive associations between prey size and owl reproductive success, but Ward and Gutiérrez (1989) could not detect such differences. The question of whether or not this association reflects abundance of prey or selection by owls (that is, either differential capture or merely differential transport of large prey to nest sites) has not been answered satisfactorily and needs field experimentation. Hansen (1987), for example, reported that offspring survival is greater for free-ranging pairs of bald eagles that are fed supplemental food than for unfed pairs. Given the tameness of spotted owls toward humans, analogous feeding experiments might be possible.

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Habitat Affinities of Prey Species

Information on the abundance and habitat affinities of five mammal species important as prey to northern spotted owls is summarized in tables J2 to J5. Studies that reported mammal abundance along or among forest seres were of primary interest. Direct, detailed comparisons among studies were often not possible because of differences in study design, objectives, or measures of abundance, which ranged from indices of relative abundance to reports of absolute density. Where necessary, measures of abundance were recalculated or data were summarized. Origins of forest stands on the study sites were classed, where possible, as “naturally regenerated” (that is, derived from fire, blowdowns, and so on) or “managed” (from logging). This distinction may become blurred where stands of natural origin receive some silvicultural treatments at young or intermediate ages. Finally, we assumed that the size-classes of trees used to characterize forest stands were roughly similar among studies (that is, seedling and saplings, 0 to 5 inches in d.b.h.; pole timber, 5 to 11 inches in d.b.h.; small saw timber, 11 to 21 inches in d.b.h.; large saw timber, 21 to 35 inches in d.b.h.; and old growth, 35 or more inches in d.b.h.). Tree diameters, however, were often not reported.

Two caveats regarding interpretation of the mammal studies seem necessary. First, most small mammal populations fluctuate notoriously in abundance over time; consequently, short-term studies—that is, most of those reported here—are often insufficient to establish broad ecological relationships (Wiens 1981). Secondly, the response of small-mammal populations to stand age may vary depending on the agents initiating the seres. Naturally regenerated forest stands, for example, may retain more structural diversity than stands regenerated by clearcut silviculture (Gilbert and Allwine, in press).

Northern Flying Squirrels

Flying squirrels are generally absent from very young forests (for example, clearcuts <20 years old) (table J2, and Gashwiler 1970). Squirrel abundances tend to increase in older forests (Carey et al. 1989), but trends are inconsistent. Several studies report no significant differences in abundance across young (about 30 to 60 years) to old-growth seres for either naturally regenerated (Aubry et al., in press) or managed stands (Raphael et al. 1986, Rosenberg 1990). Flying squirrels show sensitivity to fragmentation in Douglas-fir forests of northwestern California; they tend to decline in relative abundance as old-growth stands are reduced in size (Rosenberg and Raphael 1986).

Typical squirrel densities reported for mature and old-growth forests are 0.4 to 1.2 animals per acre. Data on squirrel densities are too limited to suggest meaningful geographic or elevational trends in abundance.

Dusky-Footed Woodrats

Woodrats are most abundant in early seral forests (for example, brushy clearcuts, and pole-timber stands), they decline in intermediate-age forests, and may increase to some degree in older forests (table J3). In northwestern California, woodrats seem positively associated with the amount of forest fragmentation, especially where hardwoods occur as components of Douglas-fir stands (Rosenberg and Raphael 1986). Preliminary information for redwood forests in northwestern California indicates that appreciable woodrat populations persist into stands of intermediate age (Kerns 1988).

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Table J2—Abundance of northern age-class flying squirrels by region and forest age-class

Region/area	Vegetation type Source	Seral stage	Squirrels (numbers)	Census technique	Index of abundance	
Washington Cascades (W)	1	Young+	0.015	1	2	1
		Mature+	0.025			
		Old	0.032			
Olympics	1	SMS*	0.2(0-0.5)	2	1	2
		Old	0.1(0.0-0.3)			
	1	SMS*	0.1-0.6	2	1	9
		Old	0.1-0.8			
Oregon Coast Range	1	SMS+	0.04(0-0.10)	2	1	3
		Old	0.35(0.21-0.71)			
	1	Young+	0.017	1	2	1
		Mature+	0.014			
		Old	0.027			
	1	Young	0.4(0.1-0.8)	2	1	2
		Old	0.7(0.1-1.9)			
Cascades	1	SMS+	0.07	1	2	4
		LAS+	0.01			
		Old	0.03			
	1	SMS*	0.9(0.7-1.4)	2	1	5
		Old	1.1(0.5-1.9)			
	1	Mature*	0.6	2	1	6
		Old	1.3(0.8-1.7)			
	1	Young+	0.028	1	2	1
		Mature+	0.010			
		Old	0.029			
California Northwest	2	Clearcut*	0	3	3	7
		POT-SMS*+	0.122			
		LAS+	0.154			
		Old	0.167			
	2	Brush/ Sapling*	0	3	3	8
		POT*	15			
		SMS*	9			
		LAS+	18			
		Old	13			

Census technique; (1) pitfall traps; (2) live-trap grids; (3) track plates.

Index of abundance: (1) mean (range) of number/acre (2) mean number/100 trap-nights; (3) percentage occurrence. Vegetation type: (1) western hemlock/Douglas-fir; (2) Douglas-fir/mixed evergreen. Seral stage: Small saw timber (SMS); pole timber (POT), large saw timber (LAS); old growth (old), managed stand (*), natural regeneration (+).

Source: (1) Carey 1989; (2) Biswell and Carey 1989; (3) Witt 1989; (4) Gilbert and Allwine, in press; (5) Rosenberg 1990; (6) Volz 1986; (7) Raphael et al. 1986; (8) Raphael 1988; (9) Carey et al. 1989.

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Table J3—Abundance of northern age-class flying squirrels by region and forest age-class

Region/area	Vegetation type Source	Seral stage	Woodrats (numbers)	Census technique	Index of abundance	
<i>Dusky-footed Woodrat</i>						
Oregon						
Coast Range	4	SMS* Old	0.02±.02SE 0	2, 3	1	3
Southern	2	SES* POT* SMS	0 0.43±.19 0.16±.16	2, 3	1	3
	2, 3	SMS* Old	0.57±1.57 0.17±.05	2, 3	1	3
California						
Northwest	1	SES* POT* SMS*+ LAS* Old	0.8 50 0 0 0.01	1	1	1
	1	Cleacut* POT* SMS+ LAS+ Old	2.7 0.2 1.2 4.4 3.4	2	2	2
<i>Bushy-tailed Woodrat</i>						
Oregon						
Coast Range	4	SMS* Old	0.2±.01 0.01±.01	2, 3	1	3
Southern	2	SMS* Old	0.44±.21 0.01±.03	2, 3	1	3
	2	SES* POT* SMS*	0.03±.03 0.19±.08 0	2, 3	1	3

Census technique: (1) belt transect and nest count, live-traps at nest; (2) live-trap grid; (3) parallel transects, live-trapped. Index of abundance; (1) mean number/hectare; (2) mean number/100 trap-nights. Vegetation type: (1) Douglas-fir/mixed evergreen; (2) mixed conifer; (3) riparian (4) western hemlock/Douglas-fir.

Seral stage: Seedling/sapling (SES); pole timber (POT); small saw timber (SMS); large saw timber (LAS); old growth (old); managed stand (*), natural regeneration (+).

Source: (1) Sakai et al. 1989; (2) Raphael 1988; (3) Carey Pers. comm.

Densities of dusky-footed woodrats range considerably, from just a few animals to >40 per acre in early pole-timber stages, to perhaps 0.4 to 1.2 per acre in large sawtimber and old growth (table J3, and Ward and Gutiérrez 1989). Substantial woodrat populations may occupy brushy riparian areas. Wallen (1982) reports densities of 18.2 animals per acre from one such site at Point Reyes, California.

Bushy-tailed Woodrats

Bushy-tailed woodrats are frequently associated with cliffs, rock outcrops, and talus, but they also occupy hollow trees and logs (Maser et al. 1981). Information on their relative abundance in different forest types or size-classes is limited (table J3).

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Table J4—Abundance of deer mice by region and forest age-class

Region/area	Vegetation type Source	Seral stage	Mice (numbers)	Census technique	Index of abundance	
Washington						
Cascades (W)	1	POT+ LAS+ Old	0.062-0.128 0.143-0.223 0.168-0.332	1, 3	1	1
Olympics	1	SMS* LAS/Old	2.5 4.8	2	1	2
	1	SMS* LAS/Old	2.9 8.1	2	1	7
Oregon						
Coast Range	1	SMS+ LAS/Old	1.2 1.9	2	1	2
	3	SMS* LAS+ Old	0.132 0.053 0.138	1	1	3
	1	YOUNG* Old	1.3 1.5	2	1	7
Cascades(W)	2	SMS+ LAS+ Old	0.08 0.04 0.10	1	1	4
	1	SMS* Old	3.8(2.0-5.8) 2.7(0.6-6.0)	2	2	5
California						
Northwest	2	Clearcut* POT* SMS* LAS+ Old	0.41 0.04 0.06 0.10 0.13	1	1	6

Census technique: (1) pitfall; (2) live-trap grids; (3) snap-trap grids.

Index of abundance: (1) mean number/100 trap-nights, (2) mean (range) of number/acre.

Vegetation type: (1) western hemlock/Douglas-fir; (2) Douglas-fir/mixed evergreen; (3) Douglas-fir.

Seral stage: Small saw timber (SMS), pole timber (POT), large saw timber (LAS), old growth (old), managed stand (*). natural regeneration (+).

Source: (1) West 1990; (2) Carey et al. 1988; (3) Corn and Bury, in press; (4) Gilbert and Allwine, in press; (5) Anthony and Rosenberg 1988; (6) Raphael 1988; (7) Carey et al. 1989.

Deer Mice

Habitat affinities for the ubiquitous deer mouse are difficult to interpret (table J4). Several early studies report deer mice to be more abundant in recent clearcuts than in old growth (Gashwiler 1970; Gilbert and Allwine, in press). Additionally, deer mice were found to be more abundant at sites with adjacent clearcuts and more edge in highly fragmented, old-growth Douglas-fir forests in California (Rosenberg and Raphael 1986).

Studies of deer mouse densities along forest seres of somewhat more advanced ages (small saw timber through old growth) report either no significant associations of deer mice with stand age (Anthony and Rosenberg 1988; Corn and Bury, in press), or greater abundances in old-growth (Aubry et al., in press; Biswell et al. 1989; Gilbert and Allwine, in press; West, in press).

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Table J5—Abundance of pitfall-trapped red tree voles by region and forest age-class

Region/area	Vegetation type	Seral stage	Voles (numbers)	Index of abundance	Source
Oregon					
Coast Range	3	Young+ Mature+ Old	0.004 0.000 0.021	1	4
Cascades (W)	1	SMS+ LAS+ Old	0 0.01 0.03	1	1
	2	Clearcut* POT LAS Old	1 1 2 13	2	2
		Young+ Mature+ Old	0.000 0.006 0.018	1	4
California					
Northwest	1	Clearcut* POT* SMS* LAS+ Old	0.04 0.05 0.05 0.08 0.10	1	3

Index of abundance: (1) mean number/100 trap-nights; (2) total number caught.

Vegetation type: (1) Douglas-fir/mixed evergreen; (2) Douglas-fir; (3) western hemlock/ Douglas-fir.

Seral stage: Small saw timber (SMS), pole timber (POD), large saw timber (LAS), old growth (old), managed stand (*), natural regeneration (+).

Source: (1) Gilbert and Allwine, in press; (2) Corn and Bury 1986; (3) Raphael 1988; (4) Carey 1989.

Generalizations are tenuous, but the deer mouse may show habitat affinities broadly parallel to those of the dusky-footed woodrat: high densities initially in clearcuts, reduced abundance in intermediate-aged stands, and increased densities in old growth. Very large fluctuations in abundance over short periods also characterize this species (for example, Gashwiler 1970).

In western Washington, the forest deer mouse shows a significant positive association with old-growth in the Western Hemlock/Douglas-Fir zone (Aubry et al., in press; West, in press).

Red Tree Voles

The red tree vole seems to be positively associated with stand age in Oregon and northwestern California (Carey 1989; Corn and Bury 1986; Gilbert and Allwine, in press; Raphael 1988), and may reach significantly greater densities in old-growth forests (Aubry et al., in press; Corn and Bury, in press; table J5). The animal seems to depend heavily on Douglas-fir for food and nest sites (Maser et al. 1981; Meiselman and Doyle, in press). Beyond the observation that red tree voles are absent from Washington, information is too limited to suggest trends in abundance by geography or elevation.

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Lagomorphs

Snowshoe hares and brush rabbits often dominate the lagomorph component of owl diets, but data on habitat affinities or densities for these species are limited. Brush rabbits are strongly associated with dense cover, have relatively small home ranges, and may be locally very abundant (Chapman 1971, Shields 1960). The amount of habitat for brush rabbits is thought to have increased markedly along brushy roadsides in forests of the Oregon Coast Range (Maser et al. 1981). Snowshoe hares may increase in clearcuts after brushy cover is established (Gashwiler 1970), but responses are very unpredictable in forests of the Pacific Northwest (Black, pers. comm.). Hare densities in Washington show a lag in response to silvicultural treatments; increases may occur 4 to 5 years after logging where clearcuts are burned, and in less time if logging slash is left unburned, (Campbell, pers. comm.).

Producing Owl Prey Through Silviculture

Species composition and densities of mammalian prey for spotted owls clearly change after disturbances on the scale of clearcut logging, even though predicting species-specific responses over time is sometimes difficult (that is, beyond the obvious, where arboreal species like flying squirrels and red tree voles are eliminated by tree removal). The possibility of deliberately manipulating prey densities in spotted owl habitat to benefit owls through silvicultural prescription deserves consideration: specifically, can silviculture produce more diverse prey bases, more abundant prey populations, or reduce fluctuations in the abundance of major prey species?

The survey of habitat affinities for prey species suggests that the ability to deliberately increase owl prey populations may differ among physiographic provinces, although no direct experimental evidence supports such speculation. A little fragmentation of the forest may benefit spotted owls in the short term in Douglas-fir mixed-evergreen or mixed-conifer forests by increasing both prey diversity and the abundance of seasonally important prey species (Carey, pers. comm.). Sakai et al. (1989) suggest that owls hunting along edges of suitable habitat in mixed-evergreen forests may prey on woodrats produced in or dispersing from adjacent clearcuts. They also note that silvicultural prescriptions (such as herbicide applications or mechanical clearing) aimed at eliminating brush or hardwoods to favor conifers may reduce woodrat populations. An alternative treatment to retain woodrats would remove competing vegetation only around individual conifers, sparing the intervening brush habitat.

Modification of clearcut logging, as currently practiced, in Western Hemlock/Douglas-Fir Zone forests would seemingly be necessary to deliberately produce or maintain certain species of owl prey. For example, Mowrey and Zasada (1984) recommend that small clearcuts (no wider than about 100 feet) with large intervening "leave strips" may be necessary to maintain flying squirrel populations in Alaska. They also recommend that "broom trees" be retained to serve as survival sites for squirrels during periods of cold weather. Deliberate removal of dense, brushy vegetation in early seral forests may result in dramatic declines in snowshoe hare abundance (Sullivan and Moses 1986). Leaving or enhancing such vegetation could presumably benefit hares or, possibly, brush rabbits. Retaining forests near rock outcrops and talus may provide the combined foraging and tree nesting sites preferred by bushy-tailed woodrats.

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A major synthesis is underway on the relation of silviculture to the ecology of animal species that “damage” forest stands in the Pacific Northwest (Black, pers. comm.). Although the aim is to manipulate silviculture to limit animal damage (Loucks et al., in press), some of the same mammals of concern to foresters are also important to spotted owls, and the information being assembled could also provide a basis for manipulating owl prey.

Although the prey base for spotted owls might be enhanced under some conditions where food is considered to limit owl densities or reproductive success, how this enhancement can be accomplished without violating the other habitat requirements of the bird is not yet clear. Manipulations that enhance prey for spotted owls also risk providing habitat well suited to predators or species presumed to be competitors of the spotted owl. Thus, the net benefits from habitat manipulation must be assessed carefully; managers who seek to deliberately manipulate prey densities must simultaneously monitor owl reproductive success and survival rates.

References

- Anthony, R. G., and D. K. Rosenberg. 1988 unpubl.** Patterns of distribution and abundance of small mammals in old- and second-growth Douglas-fir forests in the Oregon Cascades. Unpubl. rep., Oregon State Univ., Corvallis. 16pp.
- Aubry, K. B., M. J. Crites, and S. D. West. In press.** Patterns of small mammal abundance and community composition in Douglas-fir forests of Washington and Oregon. *In* L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, tech. coords. Wildlife and vegetation of unmanaged Douglas-fir forests. U.S. For. Serv. Gen. Tech. Rep.
- Barrows, C. W. 1980.** Feeding ecology of the spotted owl in California. *J. Raptor Res.* 14:73-78.
- Barrows, C. W. 1985.** Breeding success relative to fluctuations in diet for spotted owls in California. Pages 50-54 *in* R. J. Gutiérrez and A. B. Carey, eds. Ecology and management of the spotted owl in the Pacific Northwest. U.S. For. Serv. Gen. Tech. Rep. PNW-185.
- Barrows, C. W. 1987.** Diet shifts in breeding and non-breeding spotted owls. *J. Raptor Res.* 21:95-97.
- Beebe, G., and J. Schonewald. 1977.** Spotted owls near Palomar. Point Reyes Bird Observatory Newsletter 42:6-7.
- Biswell, B. L., J. G. Boulanger, and A. B. Carey. 1989 unpubl.** Comparison of small mammal abundance in climax and young forests of the Olympic Peninsula, Washington. Abstract *in* L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, tech. coords. Wildlife and vegetation of unmanaged Douglas-fir forests. U.S. For. Serv. Gen. Tech. Rep.
- Biswell, B. L., and A. B. Carey. 1989 unpubl.** Flying squirrel abundance in young and old-growth forests of the Pacific Northwest. Abstract *in* L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, tech. coords. Wildlife and vegetation in unmanaged Douglas-fir forests. U.S. For. Serv. Gen. Tech. Rep.

Appendix J: Food Habits and Prey

- Black, H. C. Pers. comm.**, FS, PNW, Portland, Oreg.
- Campbell, D. Pers. comm.**, APHIS, Olympia, Wash.
- Carey, A. B. Pers. comm.**, FS, PNW, Olympia, Wash.
- Carey, A. B., et al. 1988 unpubl.** Wildlife habitat relationships in western Oregon and Washington. U.S. For. Serv., Olympia For. Sci. Lab., unpubl. annu. prog. rep.
- Carey, A. B., et al. 1989 unpubl.** Patterns of flying squirrel and woodrat abundance: spotted owl prey base study. U.S. For. Serv., Olympia For. Sci. Lab., unpubl. annu. prog. rep., 5pp.
- Carey, A. B. 1989.** Wildlife associated with old-growth forests in the Pacific North west. *Nat. Areas J.* 9:151 -162.
- Chapman, J. A. 1971.** Orientation and homing of the brush rabbit (*Sylvilagus bachmani*). *J. Mammal.* 52:686-699.
- Corn, P. S., and R. B. Bury. 1986.** Habitat use and terrestrial activity by red tree voles in Oregon. *J. Mammal.* 67:404-406.
- Corn, P. S. and R. B. Bury. In press.** Small mammals in the Oregon Coast Range. *In* L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, tech. coords. Wildlife and vegetation of unmanaged Douglas-fir forests. U.S. For. Serv. Gen. Tech. Rep.
- Forsman, E. D., E. C. Meslow, and H. M. Wight. 1984.** Distribution and biology of the spotted owl in Oregon. *Wildl. Monogr.* 87. 64pp.
- Forsman, E. D., I. Otto, and A. B. Carey. 1989 unpubl.** Diet of spotted owls on the Olympic Peninsula, Washington, and the Roseburg District of the Bureau of Land Management. Abstract *in* L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, tech. coords. Wildlife and vegetation of unmanaged Douglas-fir forests. U.S. For. Serv. Gen. Tech. Rep.
- Gashwiler, J. S. 1970.** Plant and mammal changes on a clearcut in west-central Oregon. *Ecology* 51:1018-1026.
- Gilbert, F. F., and R. Allwine. In press.** Small mammal communities in the Oregon Cascades. *In* L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, tech. coords. Wildlife and vegetation of unmanaged Douglas-fir forests. U.S. For. Serv. Gen. Tech. Rep.
- Hansen, A. J. 1987.** Regulation of bald eagle reproductive rates in southeast Alaska. *Ecology* 68(5) :1387-1392.
- Hays, D. Pers. comm.**, WDW, Olympia, WA.
- Kerns, S. J. 1988 unpubl.** Observations of wildlife diversity on lands of the Pacific Lumber Co. Prelim. rep., Pac. Lumber Co., Scotia, Calif. 26pp.

Appendix J: Food Habits and Prey

- Kerns, S. J. 1989 unpubl.** Occurrence of spotted owls in managed timber stands on lands of the Pacific Lumber Co. Prog. rep., Pac. Lumber Co., Scotia, Calif. 43pp.
- Laymon, S. D. 1988.** The ecology of the spotted owl in the central Sierra Nevada, California. Ph.D. Dissertation. Univ. California, Berkeley. 285pp.
- Loucks, D. M., N. C. Block, M. L. Roush, and S. R. Radosevich. In press.** Animal damage assessment and management in Pacific Northwest forests: an annotated bibliography. U.S. For. Serv. Gen. Tech. Rep.
- Marshall, J. T. 1942.** Food and habitat of the spotted owl. Condor 44:66-67.
- Maser, C., B. R. Mate, J. F. Franklin, and C. T. Dyrness. 1981.** Natural history of Oregon Coast mammals. U.S. For. Serv. Gen. Tech. Rep. PNW-133. 496pp.
- Meiselman, N., and A. T. Doyle. In press.** Habitat and microhabitat selection by red tree voles. Am. Midl. Naturalist.
- Meslow, E. C., E. D. Forsman, et al. 1990 unpubl.** Ecology of spotted owls on the Willamette National Forest: habitat use and demography. Unpubl. annu. res. rep. FWS, Oregon State Univ., Corvallis.
- Miller, G. S. 1989.** Dispersal of juvenile northern spotted owls in western Oregon. M.S. Thesis. Oregon State Univ., Corvallis. 139pp.
- Mowrey, R. A., and J. C. Zasada. 1984.** Den tree use and movements of northern flying squirrels in interior Alaska and implications for forest management. Pages 351 -356 in Meehan, W. R., T. R., Merrell, and T. A. Hanley, eds. Fish and wildlife relationships in old-growth forests. Am. Inst. Fish. Res. Biol., Juneau, Alaska.
- Neal, D. L., J. Verner, G. N. Steger, and G. P. Eberline. 1989 unpubl.** A study of spotted owl home-range size and composition in the Sierra National Forest. U.S. For. Serv. Unpubl. rep. 9pp.
- Ogan, C., and H. F. Sakal. 1990 unpubl.** Spotted owl food habits. U.S. For. Serv. Redwood Sci. Lab, Arcata, Calif. Unpubl. data.
- Paton, P., C. Zabel, B. Bingham, H. Sakal, and C. Ogan. 1990 unpubl.** Examination of home-range size and habitat use of the spotted owl in the Klamath Province. U.S. For. Serv. Redwood Sci. Lab., Arcata, Calif. Unpubl. rep. L5pp.
- Raphael, M. G. 1988.** Long-term trends in abundance of amphibians, reptiles and mammals in Douglas-fir forests of northwestern California. Pages 23-31 in R. C. Szaro, K. E. Severson, and D. R. Patton, eds. Management of amphibians, reptiles and small mammals in North America. U.S. For. Serv. Gen. Tech. Rep. RM-166.
- Raphael, M. G., C. A. Taylor, and R. H. Barrett. 1986.** Smoked aluminum track stations record flying squirrel occurrence. U.S. For. Serv. Res. Note PSW-384. 3pp.

Appendix J: Food Habits and Prey

- Richards, J. E. 1989.** Spotted owl food habits and prey availability on the east slope of the Washington Cascades. M.S. Thesis. Colorado State Univ., Fort Collins. 45pp.
- Roberts, C. K. 1989 unpubl.** Pellet analysis of the California spotted owl in Sequoia and Kings Canyon National Parks. Unpubl. rep. 18pp.
- Rosenberg, D. K. 1990 unpubl.** Habitat selection and abundance of northern flying squirrels in second- and old-growth Douglas-fir forests, Oregon. Unpubl. rep. State Univ., Corvallis.
- Rosenberg, K. V., and M. S. Raphael. 1986.** Effects of forest fragmentation on vertebrates in Douglas-fir forests. Pages 263-272 in J. Verner, M. L. Morrison, C. J. Ralph, eds. Modeling habitat relationships of terrestrial vertebrates. Univ. Wisconsin Press, Madison.
- Rusch, D. H., E. C. Meslow, P. D. Doerr, and L. B. Keith. 1972.** Response of great horned owl populations to changing prey densities. J. Wildl. Manage. 36:282-296.
- Sakai, H. F., B. R. Noon, and C. A. Taylor. 1989 unpubl.** The feasibility of using an indirect counting method to determine dusky-footed woodrat (*Neotoma fuscipes*) abundance and distribution in different-aged Douglas-fir/hardwood stands of northwestern California. Unpubl. rep. U.S. For. Serv. Redwood Sci. Lab., Arcata, Calif. 16pp.
- Shields, P. W. 1960.** Movement patterns of brush rabbits in northwestern California. J. Wildl. Manage. 24:381-386.
- Smith, C. C. 1963.** First recorded breeding record of the spotted owl in British Columbia. Condor 65:440.
- Solis, D. M. 1983.** Summer habitat ecology of spotted owls in northwestern California. M.S. Thesis. Humboldt State Univ., Arcata, Calif. 168pp.
- Southern, H. N. 1970.** The natural control of a population of tawny owls (*Strix aluco*). J. Zool. 162:197-285.
- Sullivan, T. P., and R. A. Moses. 1986.** Demographic and feeding responses of a snowshoe hare population to habitat alteration. J. Appl. Ecol. 23:53-63.
- Thraillkill, J., and M. Bias. 1990 unpubl.** Diets of breeding and non-breeding California spotted owls (manuscript submitted).
- Volz, K. 1986.** Habitat requirements of northern flying squirrels in west-central Oregon. M.S. Thesis. Wash. State Univ., Pullman. 21pp.
- Wallen, K. 1982.** Social organization in the dusky-footed woodrat (*Neotoma fuscipes*): a field and laboratory study. Animal Behav. 30:1171-1182.

Appendix J: Food Habits and Prey

- Ward, J. P., and R. J. Gutl  rrez. 1989 unpubl.** Spotted owl reproduction and prey abundance in northwest California. Humboldt State Univ., Arcata, Calif. Unpubl. rep. 61pp.
- WDW. 1990 unpubl.** Food habits of spotted owls in Washington. 2pp.
- West, S. D. In press.** Small mammal communities in the southern Washington Cascades. *In* L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, tech. coords. Wildlife and vegetation of unmanaged Douglas-fir forests. U.S. For. Serv. Gen. Tech. Rep.
- Wiens, J. A. 1981.** Single sample surveys of communities: Are the revealed patterns real? *Am. Naturalist* 117:90-98.
- Witt, J. W. 1989 unpubl.** Ecological aspects of the northern flying squirrel in western Oregon. BLM, Roseburg, Oreg. Unpubl. rep. 23pp.

Analysis of Forest Service Monitoring Data

Introduction

Providing for spotted owl population viability requires an adequate amount and distribution of suitable habitat for owl pairs. Planning for owl conservation requires specifying some degree of certainty that the population will persist over some period of time. Suitable habitat must be distributed to provide for the rates of genetic and demographic interchange needed to assure numbers that will adequately minimize the risk of extinction. Suitable spotted owl habitat in California, Oregon, and Washington is found both on lands reserved from timber harvest (reserved lands), and on lands open to harvest (nonreserved lands). To meet the distributional requirements of the species, the FS considered necessary the protection of areas of suitable habitat in nonreserved lands that would provide for the needs of reproductive pairs and link the suitable owl habitat found in reserved lands (USDA 1988). Each designated “island” of suitable owl habitat was identified as a Spotted Owl Habitat Area (SOHA). Together with SOHA sites on reserved lands, this collection of SOHAs formed the SOHA network. By addressing issues of owl distribution and number, the FS proposed the SOHA network as its solution to the spotted owl viability requirement (USDA 1988). The network was designed with maximum distances among SOHAs that were believed to support a high likelihood of dispersal among them.

An important assumption of the management plan for the spotted owl was that the proportion of network SOHAs occupied by owl pairs would show no significant decline over time. Owl populations outside the network were assumed to decline because of habitat loss, but would continue to provide future alternatives should the occupancy rate within the network show a significant declining trend. The FS began a monitoring program in 1987 to check the validity of these assumptions.

A census of all owls on FS lands was impossible, so a subset of the network SOHAs and several random sample areas (RSAs) were monitored to estimate owl occupancy. The sample sizes were determined separately by physiographic province with the goal of estimating the occupancy rate with 10% precision at the 95% confidence level (Azuma et al. 1989). The RSAs were 0.7-mile-radius circles (1000 acres) located at random within National Forest lands, conditioned on the polygon area being within the geographic range of the spotted owl on each National Forest, within the elevational range of the subspecies, and excluding large bodies of water. If $\geq 50\%$ of the sample unit fell within reserved land, the RSA was categorized as reserved status.

Appendix K: Monitoring Data

The size of SOHAs varied geographically to reflect variation in spotted owl home-range sizes. The SOHA sizes ranged from 1000 acres in the Klamath and Sierra Nevada Provinces to 3000 acres on the Olympic Peninsula. The basic assumption underlying monitoring was that the occupancy rates of the two sample unit populations (network SOHAs and RSAs) were a valid index for the trends in population size and reproductive rate. Occupancy rates were proposed to be monitored through time as an index to population trends. The trends in occupancy rates are compared between the SOHAs and RSAs in an effort to evaluate the efficiency of the network.

The detailed estimates of occupancy proportions, by physiographic province and individual National Forest, are provided in O'Halloran (1989) and Simon-Jackson (1989). Our goal was to extend, not duplicate, the existing syntheses of the monitoring data for FS Regions 5 (R5) and 6 (R6). The primary focus of the analyses discussed below was to explore for relationships between SOHA or RSA occupancy status and several attributes associated with these sample units. Currently, the number of attributes is somewhat limited; for example, no fragmentation indices were available to associate with the sample units. Despite these limitations, we believe that some meaningful patterns have emerged.

Methods

Parameters Estimated

The basic variable estimated for each sample unit was "occupancy." Occupancy was defined in a variety of ways including occupancy by a single owl (either male, female, or unknown sex); a pair of owls; or a reproductive pair of owls. The parameters used in our analyses were occupancy by pairs, or occupancy by either a pair or a single bird. Although information on reproductive patterns is extremely relevant, the numbers of sample units (SOHAs or RSAs) occupied in any one year by reproductive pairs were too small for meaningful analysis. Yearly estimates of occupancy, by physiographic province or land classification (reserved, nonreserved), and changes in occupancy between years, have been reported for 1988 and 1989 (O'Halloran 1989; Simon-Jackson 1989).

In addition to the occupancy status of each SOHA or RSA, we also estimated a variety of other sample unit attributes, including latitude, longitude, acres of suitable spotted owl habitat, status (reserved or nonreserved), average elevation (R6 only), and elevational range (R6 only). For SOHA samples, acres of suitable habitat were estimated within a 2.1-mile (R6) or 1.5-mile (R5) radius of the SOHA center; for RSAs, suitable habitat was estimated within the 1000-acre circle.

Basic Sampling Scheme

The basic sampling scheme for the SOHA and RSA populations assumed N sites, of which N_1 had owls and N_2 were vacant ($N_1 + N_2 = N$). We sampled n of these N sites at random. A site was visited until an owl was detected or until six visits were completed. The likelihood of detecting an owl, given presence, can be computed from the distribution of detection frequency by visit number (Azuma et al. 1989). Based on analyses of the 1988 RSA and SOHA monitoring data, the likelihood of detecting an owl in six visits, given presence at a site, was high and ranged from 0.87 to 0.97 (Azuma et al. 1989). In each year, a binomial proportion, or the proportion of sites occupied, was estimated. Occupancy was either a single bird, a pair, or a reproductive pair; each was a different classification and was represented by the estimation of a distinct proportion. The details of the sampling design and methods of calculation are given in Max et al. (1987) and Azuma et al. (1989).

Appendix K: Monitoring Data

Analyses were conducted separately by year and Region for both the RSA and SOHA samples. Data were not combined across Regions because of slight differences in sampling methods and explanatory variables. For all analyses, occupancy status (occupied by a single or a pair of spotted owls; occupied by a pair; not occupied) was the dependent variable. We considered the sample unit attributes (for example, amount of suitable habitat) as explanatory variables. We performed three types of analyses: we compared the occupancy proportion for RSAs with <500 acres of suitable habitat to those with >500 acres; we investigated the relation between occupancy history (occupied in both 1988 and 1989; occupied in one of the 2 years; not occupied in either year) and the amount of suitable habitat with a one-way analysis of variance; and we investigated the relation between occupancy status of a sample unit and the explanatory variables with stepwise logistic regression (Neter et al. 1985:361-367).

Results

R5 and R6 RSA Analyses

Occupancy proportion conditioned on the amount of suitable habitat—An exploratory analysis was made to determine any consistent patterns of occupancy, by either pairs or any owls, with the amount of suitable habitat within the RSA. For R5, the estimated occupancy rates for RSAs with >500 acres of suitable habitat were greater than for those with less suitable habitat in both 1988 and 1989 (table K1A). When the data were partitioned by land status (reserved or nonreserved), the occupancy rates were again consistently higher, given more suitable habitat (table K1B, K1C). Data from R5 included occupancy information from both the Klamath and Sierra Nevada Provinces. Because the northern spotted owl occurred only in the Klamath Province, we investigated occupancy solely in this subset of the data. Again, occupancy rates were higher, given more suitable habitat, in both the 1988 and 1989 samples (table K1D).

For R6, as in R5, the occupancy rates were positively related to the amount of suitable habitat in both years (table K2A). This pattern remained when the data were partitioned by land status (table K2B, K2C). In terms of absolute amount, the difference between occupancy proportions, by habitat amount, was less for pairs than for all owls.

Occupancy history and the amount of suitable habitat—Based on the detection of either a single owl or a pair, no significant relation was found between the occupancy history of RSAs sampled in both years in R5 and their acreage of suitable habitat ($F = 2.09$, $P = 0.131$; table K3). The rank order by mean acreage of suitable habitat, however, suggested a positive correlation between occupancy history and the amount of suitable habitat (table K3).

The R6 data, based on the detection of either a single owl or a pair, showed a strong relation between occupancy history and the amount of suitable habitat for RSAs sampled in both years ($F = 9.81$, $P < 0.001$; table K4). RSAs with more suitable acres had higher occupancy rates and were more likely to be consistently occupied.

Appendix K: Monitoring Data

Table K1—Occupancy proportion (O) conditioned on the amount of suitable spotted owl habitat acres (SA) within a circular, 1000-acre Random Sample Area (RSA); results are based on the 1988 and 1989 monitoring data from National Forest lands in Region 5^a

Occupancy (O)	Year	Pr(O SA<500)	Pr(O SA<500)
A. Reserve and nonreserve combined			
Singles and pairs	1988	33/83 = .40	17/21 = .81
Pairs	1988	13/83 = .16	11/21 = .52
Singles and pairs	1989	48/93 = .52	24/42 = .57
Pairs	1989	15/93 = .16	12/42 = .29
B. Nonreserve only			
Singles and pairs	1988	30/66 = .45	12/15 = .80
Pairs	1988	11/66 = .17	7/15 = .47
Singles and pairs	1989	35/54 = .65	12/17 = .71
Pairs	1989	11/54 = .20	7/17 = .41
C. Reserve only			
Singles and pairs	1988	3/17 = .18	5/6 = .83
Pairs	1988	2/17 = .12	4/6 = .67
Singles and pairs	1989	13/39 = .33	12/25 = .48
Pairs	1989	4/39 = .10	5/25 = .20
D. Klamath Province only			
Singles and pairs	1988	12/42 = .29	6/8 = .75
Pairs	1988	2/42 = .05	4/8 = .50
Singles and pairs	1989	20/39 = .51	7/10 = .70
Pairs	1989	5/39 = .13	6/10 = .60

^a Sample sizes were 104 in 1988 and 135 in 1989.

Appendix K: Monitoring Data

Table K2—Occupancy proportion (O) conditioned on the amount of suitable spotted owl habitat acres (SA) within a circular, 1000-acre Random Sample Area (RSA); results are based on the 1988 and 1989 monitoring data from National Forest lands in Region 6^a

Occupancy (O)	Year	Pr(O SA<500)	Pr(O SA>500)
A. Reserve and nonreserve combined			
Singles and pairs	1988	50/130 = .38	41/54 = .76
Pairs	1988	17/130 = .13	12/54 = .22
Singles and pairs	1989	39/91 = .43	35/48 = .73
Pairs	1989	21/91 = .23	14/48 = .29
B. Nonreserve only			
Singles and pairs	1988	37/86 = .43	24/26 = .92
Pairs	1988	12/86 = .14	5/26 = .19
Singles and pairs	1989	24/58 = .41	17/25 = .68
Pairs	1989	13/58 = .22	8/25 = .32
C. Reserve only			
Singles and pairs	1988	13/44 = .30	17/28 = .61
Pairs	1988	5/44 = .11	7/28 = .25
Singles and pairs	1989	15/33 = .45	18/23 = .78
Pairs	1989	8/33 = .24	6/23 = .26

^a Sample sizes were 184 in 1988 and 139 in 1989.

Table K3—Results of an analysis of variance test of the relation between the occupancy histories of circular, 1000-acre Random Sample Areas (RSAs) and the amount of suitable spotted owl habitat; results are based on the 1988 and 1989 monitoring data from National Forest lands in Region 5^a

Source	Degrees of freedom	Sum of squares	Mean square	F-statistic	P-value
Occupancy	2	267,323	133,662	2.09	0.131
Error	75	4,801,392	64,019		
Total	77	5,068,715			

Level	Sample size	Mean	Standard deviation
0	20	256.9	230.5
1	22	338.9	234.7
2	36	400.6	274.4

^a The groups were defined as: not occupied in any year (0); occupied in either 1988 or 1989 (1); occupied in both years (2). The dependent variable was acres of suitable habitat within the 1000-acre RSA circle.

Appendix K: Monitoring Data

Table K4—Results of an analysis of variance test of the relation between the occupancy histories of circular, 1000-acre Random Sample Areas (RSAs) and the amount of suitable spotted owl habitat; results are based on the 1988 and 1989 monitoring data from National Forest lands in Region 6^a

Source	Degrees of freedom	Sum of squares	Mean square	F-statistic	P-value
Occupancy	2	1,075,791	537,896	9.81	0.001
Error	136	7,460,597	54,857		
Total	138	8,536,388			

Level	Sample size	Mean	Standard deviation
0	44	294.2	210.1
1	35	411.4	236.2
2	60	500.0	249.2

^a The groups were defined as: not occupied in any year (0); occupied in either 1988 or 1989 (1); occupied in both years (2). The dependent variable was acres of suitable habitat within the 1000-acre RSA circle.

The relation between occupancy status and the explanatory variables—From the R5, 1988 occupancy data, the stepwise logistic regression model selected both land status and acres of suitable habitat as significant predictor variables (table K5A). The model interpretation suggested that the probability of detection, of either a single owl or a pair, increased with both the amount of suitable habitat and in nonreserved lands. For the 1989 sample, only land status was selected as a significant predictor of occupancy; consistent with 1988, the probability of owl detection increased in nonreserved lands (table K56).

For the 1988 R6 sample, three variables were selected as significant predictors of occupancy likelihood (table K6A). The probability of detecting an owl increased with the amount of suitable habitat, was higher in nonreserved lands, and was higher at lower latitudes. In the 1989 sample, only acres of suitable habitat was a significant, positive predictor of occupancy likelihood (table K6A).

R5 and R6 SOHA Analyses

Occupancy history and the amount of suitable habitat—we detected no relation between pair-occupancy history and amount of suitable habitat for either the R5 (table K7) or R6 (table K8) SOHA samples.

The relation between occupancy status and the explanatory variables—For the R5 SOHA samples, no variables were selected in the logistic regression of pair occupancy on the explanatory variables in either 1988 or 1989. In the R6 samples, pair occupancy was significantly related to latitude in 1988 (table K9A) and to longitude in 1989 (table K9B). Model interpretation from these years suggests that pair occupancy was higher at inland sites in mid to southern Oregon (Southern Cascades and Klamath Province).

Our findings suggest that this assumption may be invalid, we encourage increased inventory efforts in reserve lands to further explore their potential to support spotted owls.

Appendix K: Monitoring Data

Table K5—Results of the stepwise logistic regression analysis of the occupancy status of circular, 1000-acre Random Sample Areas (RSAs) and a number of predictor variables; results are based on the 1988 (A) and 1989 (B) monitoring data 1 mm National Forest lands In Region 5^a

A. 1988 results

Variable	Coefficient	P-value
Status	0.6086	0.065
Acres	-0.0044	0.001
Constant	1.5932	0.001

Model:

$$\text{Pr(no owls detected)} = \exp[1.59 - 0.0044(\text{acres}) + 0.61 (\text{status})] / (1 + \exp[1.59 - 0.0044(\text{acres}) + 0.61 (\text{status})])$$

Model interpretation:

Pr(owls detected) increased: a) with the amount of suitable habitat,
b) in nonreserve lands

B. 1989 results:

Variable	Coefficient	P-value
Status	0.5584	0.002
Constant	-0.1137	0.530

Model:

$$\text{Pr(no owls detected)} = \exp[-0.11 + 0.56(\text{status})] / (1 + \exp[-0.11 + 0.56(\text{status})])$$

Model interpretation:

Pr(owls detected) increased in nonreserved lands

^a The dependent variable was occupancy status (0 = no owls detected; 1 = single or pair detected). Possible predictor variables for selection were land status, acres of suitable habitat, latitude, and longitude, sample sizes were 104 in 1988 and 135 in 1989.

Appendix K: Monitoring Data

Table K6—Results of the stepwise logistic regression analysis of the occupancy status of circular, 1000-acre Random Sample Areas (RSAs) and a number of predictor variables; results are based on the 1988 (A) and 1989 (B) monitoring data from National Forest lands in Region 6^a

A. 1988 results

Variable	Coefficient	P-value
Status	0.4935	0.008
Acres	-0.0041	0.001
Latitude	0.1877	0.020
Constant	-6.8735	0.057

Model:

$$\text{Pr(no owls detected)} = \exp[-6.87 - 0.0041(\text{acres}) + 0.49(\text{status}) + 0.19(\text{latitude})] / (1 + \exp[-6.87 - 0.0041(\text{acres}) + 0.49(\text{status}) + 0.19(\text{latitude})])$$

Model interpretation:

Pr(owls detected) increased: (a) with the amount of suitable habitat
(b) in nonreserve lands
(c) at lower latitudes

B. 1989 results:

Variable	Coefficient	P-value
Acres	-0.0028	0.001
Constant	0.9921	0.006

Model:

$$\text{Pr(no owls detected)} = \exp[0.99 - 0.0028(\text{acres})] / (1 + \exp[0.99 - 0.0028(\text{acres})])$$

Model Interpretation:

Pr(owls detected) increased with the amount of suitable habitat

^a The dependent variable was occupancy status (0= no owls detected; 1 = single or pair detected). Possible predictor variables for selection were land status, acres of suitable habitat average elevation, elevational range, latitude, and longitude. Sample sizes were 184 in 1988 and 139 in 1989.

Appendix K: Monitoring Data

Table K7—Results of an analysis of variance test of the relationship between the pair-occupancy histories of Spotted Owl Habitat Areas (SOHAs) and the amount of suitable habitat; results are based on the 1988 and 1989 monitoring data from National Forest lands in Region 5^a

Source	Degrees of freedom	Sum of squares	Mean square	F-statistic	P-value
Occupancy	2	32,440	16,220	0.07	0.932
Error	108	24,861,152	230,196		
Total	110	24,893,584			

Level	Sample size	Mean	Standard deviation
0	25	1060.2	545.6
1	33	1039.5	385.3
2	53	1079.3	499.3

^a The groups were defined as: not occupied in any year (0); occupied in either 1988 or 1989 (1); occupied in both years (2). The dependent variable was acres of suitable habitat within a 1.5-mile radius of the SOHA center.

Table K8—Results of an analysis of variance test of the relation between the pair-occupancy histories of Spotted Owl Habitat Areas (SOHAs) and the amount of suitable habitat; results are based on the 1988 and 1989 monitoring data from National Forest lands in Region 6^a

Source	Degrees of freedom	Sum of squares	Mean square	F-statistic	P-value
Occupancy	2	3,722,675	1,861,338	1.08	0.340
Error	190	326,258,176	1,717,148		
Total	192	329,980,672			

Level	Sample size	Mean	Standard deviation
0	57	3029	1301
1	72	3370	1315
2	64	3233	1313

^a The groups were defined as: not occupied in any year (0); occupied in either 1988 or 1989 (1); occupied in both years (2). The dependent variable was acres of suitable habitat within a 2.1-mile radius of the SOHA center.

Appendix K: Monitoring Data

Table K9—Results of the stepwise logistic regression analysis of the pair-occupancy status of Spotted Owl Habitat Areas (SOHAs) and several predictor variables; results are based on the 1988 (A) and 1989 (B) monitoring data from National Forest lands in Region 6^a

A. 1988 results

Variable	Coefficient	P-value
Latitude	0.1487	0.099
Constant	-6.9464	0.084

Model:

$$\text{Pr}(\text{no owls detected}) = \exp[-6.95 - 0.1487(\text{latitude})] / (1 + \exp[-6.95 + 0.1487(\text{latitude})])$$

Model interpretation:

Pr(owls detected) increases at lower altitudes

B. 1989 results:

Variable	Coefficient	P-value
Longitude	0.3383	0.020
Constant	-8.0595	0.013

Model:

$$\text{Pr}(\text{no owls detected}) = \exp[-8.06 + 0.34(\text{longitude})] / (1 + \exp[-8.06 + 0.34(\text{longitude})])$$

Model Interpretation:

Pr(owls detected) increases with decreasing longitude (that is, away from the coast)

^a The dependent variable was occupancy status (0 no owl pair detected; 1 = owl pair detected). Possible predictor variables for selection were land status, acres of suitable habitat, average elevation, elevational range, latitude, and longitude. Sample sizes were 136 in 1988 and 192 in 1989.

Discussion

The RSA sample data provided the most useful insights into the correlation between site occupancy and a number of possible explanatory variables. The association of SOHA occupancy status with these same variables may have been weaker because of the purposeful placement of SOHA sites. To a large extent, SOHAs were placed around known pairs of spotted owls and in sites with relatively large amounts of suitable habitat. As a consequence, the observed variation in occupancy, and in the explanatory variables, was less than in the RSA sample. The RSA samples more accurately reflected the magnitude of variation in landscape and habitat attributes and their relation to occupancy status.

Analyses of RSA data showed consistent and strong, positive associations between the amount of suitable habitat and occupancy by either pairs or single birds. Further, the results indicated the likelihood of consistent occupancy across years was related to the amount of suitable habitat within the RSA. Land status was also selected as a significant predictor in three of four logistic regression analyses. These results indicated that occupancy was higher in nonreserved lands; that is, lands available for timber harvest. We believe this finding is significant. The current SOHA management plan for the spotted owl (USDA 1988) puts great emphasis on the capacity of reserve lands (primarily Wilderness Areas) to support large numbers of spotted owls.

Appendix K: Monitoring Data

Geographical position (latitude and longitude) was also related to occupancy. In both the RSA and SOHA samples in R6. Collectively, these results suggested a significantly lower likelihood of occupancy. In both SOHAs and random sites, in the Coast Range of Oregon and the Olympic Peninsula in Washington. Further, an independent analysis (Noon, pers. comm.) demonstrated that fecundity rates were significantly lower in the Oregon Coast Range province. The finding of both lower occupancy rates and fecundity values indicate that these locations should be given special consideration when designating the number and size of HCAs needed for an effective conservation strategy.

References

- Azuma, D., J. Baldwin, and B. R. Noon. 1989 unpubl.** A sampling scheme for estimating occupancy of spotted owl habitat areas (SOHAs). Manuscript. U.S. For. Serv., Pacific Southwest Region, Berkeley, Calif.
- Max, T. A., R. A. Souter, and K. A. O'Halloran. 1987 unpubl.** Statistical estimators for monitoring spotted owls in Oregon and Washington. U.S. For. Serv., Pacific Northwest Region, Portland, Ore.
- Neter, J., W. Wasserman, and M. H. Kutner. 1985.** Applied linear statistical models. R. D. Irwin, Inc., Homewood, Ill. 1127pp.
- Noon, B. Pers. comm.** FS, PSW, Arcata, Calif.
- O'Halloran, K. 1989 unpubl.** Spotted owl inventory and monitoring: Annual report for 1989. U.S. For. Serv., Pacific Northwest Region, Portland, Ore. 13pp.
- Simon-Jackson, T. 1989 unpubl.** Spotted owl inventory and monitoring program: Annual report for 1989. U.S. For. Serv., Pacific Southwest Region, San Francisco, Calif. 10pp.
- U.S. Department of Agriculture, Forest Service. 1988.** Final supplement to the environmental impact statement for an amendment to the Pacific Northwest regional guide. Two volumes. U.S. For. Serv. Portland, Ore.

Estimates of Demographic Parameters and Rates of Population Change

Introduction

Standard Lotka-Leslie (Lotka 1956, Leslie 1945, 1948) methodology was applied to the estimates of the vital rates to make inferences to rates of population change from three geographic locations. We assumed that reproduction was characteristic of a birth-pulse population (Caughley 1977:6). Further, the analyses presented below assumed no density-dependence, were based on a 1:1 sex ratio at birth, and were formulated exclusively in terms of females.

Following standard representation, the basic demographic life history of the spotted owl is presented in table L1. The parameter b_x denotes the expected number of female fledglings produced by a female of age x . Because the ages of females breeding, or attempting to breed, are seldom known, we assumed $b_x = b$ ($x \geq 2$ yrs). The parameter l_x represents the probability of survival to age x (by definition $l_0 = 1.0$). The number of age-classes for which annual survival probabilities were assumed to be distinct was three; 1st (s_0 [juvenile]) and 2nd (s_1 [subadult]) years, and adults (s). Probability of survival to age x is thus given by $l_x = s_0 s_1 s^{x-2}$ (table L1). For these analyses, we did not partition 1st-year survival into predispersal and postdispersal probabilities as was done by Lande (1988). Parameter estimates used in our analyses of the three locations are given in tables L2 to L4.

Table L1—Spotted owl life history (age at first reproduction = 2 years)

x^a	l_x^b	b_x^c	$l_x b_x^d$
0	1.0	0	0
1	s_0	0	0
2	$s_0 s_1$	b	$s_0 s_1 b$
3	$s_0 s_1 s$	b	$s_0 s_1 s b$
4	$s_0 s_1 s^2$	b	$s_0 s_1 s^2 b$
•	•	•	•
•	•	•	•
•	•	•	•
x	$s_0 s_1 s^{x-2}$	b	$s_0 s_1 s^{x-2} b$

^a x denotes age expressed in years.

^b l_x denotes the probability that an individual aged 0 (a newly hatched bird) will survive to enter age-class x .

^c b_x denotes the expected number of female fledglings produced by a surviving female aged x .

^d $l_x b_x$ denotes the net maternity function.

Appendix L: Population Change

Table L2—Ninety-five percent confidence intervals on λ and tests of the hypothesis that $\lambda \geq 1.0$ based on parameter estimates from Six Rivers National Forest, California, 1985-89 (Franklin et al. 1990a)

Parameter	Estimate	Sample size	Standard error	Sensitivity	
				a	b
s_0^a	0.138	63	0.046	0.305	
s_0^b	0.290	17	0.110		0.280
s_1	0.903	34	0.024	0.046	0.090
s	0.903	164	0.024	0.956	0.918
b	0.335	280	0.046	0.126	0.243
λ^a	0.947		0.027		
λ^b	0.991		0.039		

$(a)\lambda \pm (Z_{.05})6\lambda$
 $0.947 + (1.96)(0.027)$
 $(0.893 - 1.000)$
 $Z = |(0.947 - 1)/0.027| = 1.924, P < 0.027$

Conclusion: reject H_0 .

$(b)\lambda \pm (Z_{.05})6\lambda$
 $0.991 + (1.96)(0.039)$
 $(0.914 - 1.069)$
 $Z = |(0.991 - 1)/0.039| = 0.2152, P = 0.415$

Conclusion: do not reject H_0 .

Table L3—Ninety-five percent confidence intervals on λ and test of the hypothesis that $\lambda \geq 1.0$ based on parameter estimates from Roseburg District, BLM, Oregon, 1986-89 (Forsman, pers. comm.)

Parameter	Estimate	Sample size	Standard error	Sensitivity
s_0	0.219	181	0.072	0.201
s_1	0.588	44	0.086	0.046
s	0.812	213	0.025	0.959
b	0.310	215	0.115	0.115
λ	0.858		0.033	

$\lambda \pm (Z_{.05})6\lambda$
 $0.873 \pm (1.96)(0.038)$
 $(0.798 - 0.948)$
 $Z = |(0.8731 - 1)/0.0283| = 3.3091, P < 0.005$

Conclusion: Reject H_0 .

Appendix L: Population Change

Table L4—Ninety-five percent confidence intervals on λ and test of the hypothesis that $\lambda \geq 1.0$ based on parameter estimates from Olympic National Forest, Washington, 1987-89 (Forsman, pers. comm.)

Parameter	Estimate	Sample size	Standard error	Sensitivity
s_0	0.150	n/a	0.050	0.299
s_1	0.935		0.035	0.041
s	0.935	96	0.035	0.960
b	0.280	47	0.216	0.138
λ	0.975		0.047	

$$\lambda \pm (Z_{.05})6_{\lambda}$$

$$0.975 \pm (1.96)(0.047)$$

$$(0.882 - 1.068)$$

$$Z = |(0.975 - 1)/0.047| = 0.521, P < 0.302$$

Conclusion: Do not reject H_0 .

In our analyses, “adult” referred to ages subsequent to the 2nd year of life; within this age-class, survival rate was assumed constant. Pre-adult survival rate (l_2) represented the probability of survival from fledging to age 2 and was given by the product of s_0 and s_1 .

Estimates of the rates of population change from the basic demographic life table (table L1) required the estimation of five parameters, s_0 , s_1 , s , b , and a (age at first reproduction). Preliminary estimates of these parameters were available for all three studies analyzed here. Because these terms were expected to vary geographically, separate analyses were conducted.

Estimates of all the parameters needed for a completely age-specific Leslie matrix were unavailable. With long-lived species, data are often limited, and estimates of all the age-specific parameters are impossible to attain or have large sampling variances because of small sample sizes. Repeated multiplication of imprecise estimates in fully age-specific models is likely to lead to uncontrolled error propagation (Dobson and Lyles 1989). A useful approximation to an age-structured model is a stage-structured model called a Lefkovich matrix (Lefkovich 1965). Structurally, the dynamics of the two models are usually very similar, but the Lefkovich model is more tractable (Boyce 1987). Estimating the population dynamics of spotted owls with a stage matrix would yield misleading conclusions only if the species experienced reproductive senescence before about 15 years (Noon and Biles 1990). Given the current high estimates for s , early senescence seemed unlikely. For spotted owls, we divided the population into three stages, juveniles, J ; subadults, S ; and adults, A . Time was expressed on an interbirth interval of 1 year, and we assumed an age at first reproduction of 2 years. Given that spotted owl populations were censused shortly after the birth-pulse, the Lefkovich matrix had the following structure:

$$\begin{bmatrix} J_{t+1} \\ S_{t+1} \\ A_{t+1} \end{bmatrix} = \begin{bmatrix} 0, & s_1 b & s b \\ s_0, & 0, & 0 \\ 0, & s_1, & s \end{bmatrix} \begin{bmatrix} J_t \\ S_t \\ A_t \end{bmatrix}$$

Appendix L: Population Change

The location of s along the diagonal of the matrix reflects our assumption of constant adult survival and no senescence. The possibility of very old owls in the population had no effect on our estimate of population growth rate (λ), assuming that adult survival was estimated irrespective of adult age from an unbiased sample of all adults in the population (Boyce 1987). For all three studies, we believe this assumption was valid.

The basic characteristic equation of the matrix is given by

$$\lambda^2 - s\lambda - s_0s_1b = 0. \quad (1)$$

Equation (1) has two solutions; the dominant, real-valued solution (λ_1) is an estimate of the annual rate of change of the population. If $\lambda > 1.0$, the vital rates suggest the population was increasing; if $\lambda = 1.0$, the population size was stable; and if $\lambda < 1.0$, the population was declining. We urge caution in using the computed estimates of λ (tables L2 to L4) to forecast future population sizes or to infer the size of historical populations. Lambda was merely an estimate of how the population was changing over the period of study. Using the estimate of λ to project future population size must be based on the unrealistic assumption that current estimates of the vital rates remain constant. Populations governed by Leslie or Lefkovich matrices grow, or decline, exponentially (except for the unlikely case where $\lambda = 1.0$). This model is clearly unrealistic for the long-term growth or decline of any natural population. For example, all growing populations experience density-dependent limitation when they reach the carrying capacity of their environment.

Methods— Hypothesis Tests on Lambda

Estimates of the demographic characteristics of spotted owls were available from three locations: Klamath Province, Six Rivers National Forest (Franklin et al. 1990), Oregon Coast Range Province, Roseburg, Oregon District of the BLM (Forsman, pers. comm.), and Olympic Peninsula, Olympic National Forest (Forsman, pers. comm.). In all three study areas, estimates of age-specific survival rates, ages at first reproduction, and adult fecundity were based on the histories of banded birds. For the California (Franklin et al. 1990a) and Oregon (Forsman, pers. comm.) studies, estimates of adult female survival rates (s) were based on the methods of Jolly (1965) and Seber (1965) and assumed an open population. For Forsman's study on the Olympic Peninsula, data were too sparse for Jolly-Seber estimates. Survival rates were estimated empirically with the subadult and adult age-classes combined across the sexes. First-year survival rate (s_0) was estimated empirically in all studies. The demographic studies varied in duration from 3 (Olympic Peninsula) to 5 (Oregon) to 6 (California) years.

The sensitivities (partial derivatives) of λ with respect to the individual life-history characteristics indicate which of the parameters most affects variation in the population growth rate (Lande 1988, Noon and Biles 1990). In addition, sensitivities are needed to estimate the standard error of λ and to perform hypothesis tests. Sensitivities were computed by implicit differentiation of the characteristic equation (Goodman 1971, Lande 1988). Sensitivities for spotted owl parameters are:

$$\begin{aligned} s_0: \partial\lambda / \partial s_0 &= s_1b / (2\lambda - s); \\ s_1: \partial\lambda / \partial s_1 &= s_0b / (2\lambda - s); \\ s: \partial\lambda / \partial s &= \lambda / (2\lambda - s); \text{ and} \\ b: \partial\lambda / \partial b &= s_0s_1 / (2\lambda - s). \end{aligned}$$

Appendix L: Population Change

The values of the sensitivity coefficients for the three geographic areas are given in tables L2 to L4. For all areas, change in population growth rate was most sensitive to variation in adult survival rate, and next most sensitive to variation in the 1st-year survival rate (Lande 1988, Noon and Biles 1990).

The sensitivities of λ appear in the formula that approximates the sampling variance of the λ estimate (Lande 1988:602):

$$6^2_{\lambda} = \sum (\partial\lambda/\partial\pi)^2 6\pi^2 \quad (2)$$

where π represents each of the parameters and $6\pi^2$ their sampling variance. Following Lande (1988), we assumed the survival probabilities for the Washington study, and for the 1st- and 2nd-year survival rates for California and Oregon, had binomial sampling distributions and computed their variance as $6\pi^2 = \pi(1 - \pi)/N\pi$. The variances of the adult survival rates from California and Oregon were estimated according to the methods of Jolly (1965) and Saber (1965). The variance of the annual fecundity was based on the variance among females across the years of study divided by the appropriate sample size.

Equation (2) neglects possible covariances among the demographic parameters and fails to account for between-year changes in the vital rates. Between-year changes, estimated by factoring out the temporal component of variation from the total variance estimates of the vital rates and λ , are currently being estimated for the California data (Noon, pers. comm.).

The components of the sampling variance of λ were computed by using equation (2), based on the sensitivities and estimates of the vital rates given in tables L2 to L4. The standard error of λ , computed as the square root of the variance, was used to construct a confidence interval around λ . For example, the 95% confidence interval on λ was computed as: $\lambda \pm (1.96)(6_{\lambda})$. An estimate of λ and its standard error also allowed tests of hypotheses. Of most interest, relative to concern for the species' persistence, was whether λ was significantly <1.0 . Tests were conducted as one-tailed tests of the hypothesis: $H_0: \lambda \geq 1$, versus the alternative hypothesis: $H_A: \lambda < 1$. The appropriate test statistics followed a Z-distribution and was given by: $Z = |(\lambda - 1)/6_{\lambda}|$. Tests were one-tailed with a specified probability of a Type 1 error = 0.05.

Estimates of survival and reproductive rates used in the subsequent demographic analyses were based exclusively on banded birds. In some studies, backpack-mounted radio transmitters appeared to affect reproduction (Foster et al. unpubl.) or both survival and reproduction (Paton et al. unpubl.). For this reason, we did not include information from any birds with radio transmitters.

Results—Tests on Lambda

We report results from two different analyses of the demographic parameters from California (table L2). They differ in the estimate used for 1st-year survival, and its associated standard error and sensitivity coefficient. In scenario b, we used $s_0 = 0.290$, the maximum survival rate observed for a juvenile cohort (1985 cohort; Franklin et al. 1990a). The estimate of adult survival we used ($s = 0.903$) differed from that reported in Franklin et al. (1990). Our estimate was based on a reanalysis of Franklin's data (Anderson and Franklin, pers. comm.).

Appendix L: Population Change

Based on the vital rates for scenario a ($s_0 = 0.138$; $s = 0.903$), $\lambda = 0.947$ and, by a one-tailed test, was significantly <1.0 ($P = 0.027$). This value of λ suggests that the study population in northwestern California was undergoing a significant population decline during the period 1984-89. If the vital rates were to remain constant, this value of λ suggests an annual rate of population decline equal to 5.3% ($[1 - \lambda] \times 100\%$). This estimated rate of decline slightly exceeded the estimated rate of loss of suitable owl habitat from the study area over the interval 1985-88 (Franklin et al. 1990b).

The estimate of s_0 from the 1985 cohort may be more reliable because of the increased opportunity to have reobserved these color-marked individuals. Based on this consideration, when we used the more optimistic estimate for s_0 , (0.290), λ was still <1.0 ($\lambda = 0.991$) but was no longer significant ($P = 0.415$). Conditioned on constant parameter values, a $\lambda = 0.991$ suggests a 0.9% annual rate of population decline.

Based on the estimates of the vital rates for the Oregon BLM land, $\lambda (= 0.858)$ was significantly <1.0 ($P < 0.001$). This estimate suggests that the study population in the Oregon Coast Range had undergone a significant population decline during the period 1986-89. If the vital rates were to remain constant, this value of λ suggests an annual rate of population decline equal to 14.1%. The sensitivities (table L2) indicate that the low value of λ was most attributable to the low adult survival rate (s). A portion of the estimated decline in population may have been attributable to loss of suitable habitat. From 1986-89, the estimated rate of loss, from BLM lands, of mature and old-growth forest on the study area was 5.1% (Lint, pers. comm.). This was a minimum estimate of the rate of loss. A large portion of the study area included private timber lands that were heavily harvested during the period of study and from which no data were available.

Estimates of the vital rates for the Olympic Peninsula yielded a $\lambda = 0.975$, which was not significantly <1.0 ($P = 0.302$). Because λ could not be demonstrated to be significantly <1.0 , these data did not support the conclusion that the spotted owl population had experienced a significant population decline during the interval 1986-89. If the vital rates were to remain constant, however, this value of λ suggests an annual rate of population decline equal to 2.5%. The results of this analysis must be interpreted cautiously because they are based on only 3 years of study and as a result, rely on small sample sizes and imprecise parameter estimates (table L3). In addition, we were unable to develop a female-based model for this study because insufficient data were available from adult female owls. If female owls on the Olympic Peninsula had lower survival rates than males, as they did in northwestern California over a similar period of study (Franklin et al. 1990a), then our estimate of λ was too high.

Discussion

All three demographic study areas—Klamath Province in California, Coast Range in Oregon, and the Olympic Peninsula in Washington—yielded estimates of $\lambda < 1.0$, which suggested that, in all three areas, spotted owl populations had experienced declines. The λ estimates from California and Oregon, the studies of longest duration and with largest sample sizes, were statistically significant.

Appendix L: Population Change

Estimates of parameter sensitivities from all three study areas suggests that λ values were most sensitive to estimates of adult survival rate (s), distantly followed by 1st-year survival rate (s_0) and fecundity (b). The sensitivity coefficient associated with age at first reproduction (a), which was not reported here, was <0.0001 (Noon and Biles 1990). Note, however, that two sources of information are relevant to a species' rate of population change (λ): one is the sensitivity of λ to variation in the vital rates as reflected in parameter sensitivity coefficients; and the other concerns those life-history attributes that show the most natural variation. Variations in growth rate (λ) may be more closely associated with attributes that are naturally more variable than to attributes that are less variable but to which growth rate is more sensitive in a mathematical sense. Estimates of the magnitude of natural variation in demographic parameters are just now becoming possible. Preliminary analyses of data from the Klamath Province of California (Franklin et al. 1990a) suggest that true, year-to-year variation in λ may have been most attributable to annual variation in 1st-year survival rate (Noon, pers. comm.).

On the surface, the separate estimate of population trend from the California study area (Franklin et al. 1990b) appears to contradict inferences from the estimate of λ (0.947) for the same population. To understand this apparent contradiction, several points are particularly relevant. First, when the demography of spotted owls is studied, the sampled population in a given field season consists almost entirely of territorial birds and their offspring. Nonterritorial (floater) birds were seldom captured unless they eventually entered the territorial population. Thus, the estimates of the vital rates were based almost exclusively on the dynamics of the territorial population.

Second, all of the spotted owl demography studies have taken place in areas that experienced declines in the amount of suitable habitat during the study period (Franklin et al. 1990b; Forsman, pers. comm.). Assuming some degree of site fidelity, territorial spotted owls displaced by habitat loss would then enter a local floater population. Local populations have additional sources of floaters, particularly from areas experiencing habitat loss. These floaters include juvenile and subadult birds unable to find a vacant territory or a mate.

Third, the Jolly-Saber model used to estimate population size (Franklin et al. 1990b) did not discriminate between internal recruitment events resulting from natality, and those that were a consequence of immigration into the territorial population. In contrast, the estimate of b used in the computation of λ (equation 1) reflected only the internal recruitment (natality) potential of the territorial birds. Thus, even a territorial population whose death rate far exceeded its birth rate could remain relatively stable over the short-term if it experienced rapid replacement of territorial birds by floaters. Estimates of λ from demographic models, however, are functions of a population's survival and fecundity rates. As a result, λ estimates discriminate between population stability from the recruitment of floaters and stability from an internal balance between birth and death rates. The λ estimate from Franklin's study indicates that the death rate of the territorial population exceeded its birth rate.

Appendix L: Population Change

Immigration into a territorial population can occur from both inside and outside the general study area. In northwestern California, the age distribution of new recruits into the population, which strongly favors adults (Franklin et al. 1990b), suggests that the observed increases in population size resulted from immigration. The source of the adult immigrants could have been from outside the study area, or from birds floating within the study area for two or more years. We think a plausible explanation for Franklin's results is one that attributes much of the population increase to recruitment of birds from outside the study area, possibly the result of an influx of individuals displaced by timber harvest.

The Jolly-Seber model provides estimates of the magnitude of annual recruitment into a population. The difference between this estimate and that portion attributable to internal natality (b) is even more dramatic in the Oregon Coast Range than in northwestern California (Anderson and Forsman, pers. comm.). In contrast, however, the new recruits into the territorial population in Oregon were an even mix of subadult and adult birds (Meslow, pers. comm.). Forsman and Meslow (pers. comm.) believe the age-ratio data suggest immigration into the territorial population from both inside and outside their study area. During the period of study (1986 to 1989), the Oregon Coast Range, including Forsman's study area, experienced extensive harvest of suitable spotted owl habitat.

An additional consideration, particularly relevant for a species like the spotted owl, argues strongly for the use of estimates of demographic parameters to infer the rate and direction of population change. A long-lived species experiencing a rapid decline in suitable habitat may show an increased density from the packing of individuals in the remaining habitat. Even though these nonterritorial individuals (floaters) do not contribute to the breeding population, they may have significant negative impacts on population dynamics because of density-mediated declines in the survival and fecundity rates of the territorial birds. Such declines could occur, for example, as a result of localized prey depression. For example, studies of the tawny owl demonstrated density-dependent declines in reproductive success, and related the declines to changes in prey availability (Southern 1970). The existence of floaters can also introduce a lag in detecting declines in the territorial population. This lag occurs because floaters quickly replace territorial birds that die, making the territorial population appear stable.

Based on the two studies of spotted owl demography that provide reliable survival rate estimates (Klamath Province, California (Franklin et al. 1990a); Oregon Coast Range (Forsman, pers. comm.)), we accept the hypothesis that spotted owl populations were declining ($\lambda < 1.0$) in parts of their range from 1985-89. Further, if the vital rates estimated from these two populations remained the same, these populations would continue to decline in the future.

Acknowledging the possibility of a Type 2 error is important, if the survival rate estimates were negatively biased. Bias can occur if a large number of banded birds permanently left the study area and survived. We believe this was likely for 1st-year birds because they were the most likely to emigrate, but not for adults. Given the relatively low sensitivity of λ to s and, in contrast, λ 's extreme sensitivity to s , that the estimates of λ were appreciably affected by any confounding of mortality with permanent emigration is unlikely.

Appendix L: Population Change

Studies of radio-marked, adult spotted owls provided a way of estimating the magnitude of permanent emigration. To make this estimate, we computed the number of emigrations per bird-year. A bird-year was defined as one adult bird tracked for one calendar year. From radio-telemetry studies near Roseburg, Oregon, only one occurrence of permanent emigration was recorded in >100 bird-years (Forsman, pers. comm.). Radio-telemetry studies in northwestern California recorded one permanent emigration in 60 bird-years (Paton, pers. comm.). These findings suggest that the estimates of adult survival rate were not affected by permanent emigration from the study areas.

The most ready explanation for the apparent population decline in northwestern California (Franklin et al. 1990a) and the Oregon Coast Range (Forsman, pers. comm.) was the decline in the amount of suitable owl habitat during the study period. This explanation, however, only partially accounts for the magnitude of the population decline. In addition to the decline predicted from the absolute amount of habitat loss, the spatial arrangement of the remaining habitat must also be considered. Habitat that is widely dispersed and isolated into small blocks may be unoccupied because of the low probability of successful dispersal to those patches, and because of higher pair turnover rates. The difficulty of finding suitable habitat that has both a vacant territory and an individual of the opposite sex, might quickly become insurmountable in a highly fragmented landscape. The influence of these factors on the owl's population dynamics are explored in appendix M.

References

- Anderson, D., and E. D. Forsman. Pers. comm.** FWS, Cob. State Univ., Fort Collins, and FS, PNW, Olympia, Wash.
- Anderson, D., and A. Franklin. Pers. comm.** FWS, Cob. State Univ., Fort Collins, and Dep. Wildlife, Humboldt State Univ., Arcata, Calif.
- Boyce, M. S. 1987 unpubl.** A review of the U.S. Forest Service's viability analysis for the spotted owl. Final report to the National Council of the Paper industry for Air and Stream improvement. 50pp.
- Caughley, G. 1977.** Analysis of vertebrate populations. John Wiley and Sons, New York. 234pp.
- Dobson, A. P., and A. M. Lyles. 1989.** The population dynamics and conservation of primate populations. *Conserv. Biol.* 3:362-380.
- Forsman, E. D. Pers. comm.** FS, PNW, Olympia, Wash.
- Foster, C., E. D. Forsman, E. C. Meslow, G. S. Miller, and A. B. Carey. Unpubl.** The effects of radio backpacks on the survival and reproduction of the northern spotted owl in Oregon and Washington. Ms. in prep.
- Franklin, A. B., J. A. Blakesley, and R. J. Gutiérrez. 1990a.** Population ecology of the northern spotted owl in northwestern California: Preliminary results, 1989. Final report submitted to the U.S. For. Serv and the Calif. Dep. Fish and Game. 31pp.

Appendix L: Population Change

- Franklin, A. B., J. P. Ward, R. J. Gutiérrez, and G. I. Gould, Jr. 1990b.** Density of northern spotted owls in northwestern California. *J. Wildl. Manage.* 54:1-10.
- Goodman, L. A. 1971.** On the sensitivity of the intrinsic growth rate to changes in the age-specific birth and death rates. *Theoret. Popul. Biol.* 2:339-354.
- Jolly, G. M. 1965.** Explicit estimates from capture-recapture data with both death and dilution-stochastic model. *Biometrika* 52:225-247.
- Lande, R. 1988.** Demographic models of the northern spotted owl (*Strix occidentalis caurina*). *Oecologia* 75:601-607.
- Lefkovich, L. P. 1965.** The study of population growth in organisms grouped by stages. *Biometrics* 21:1-18.
- Leslie, P. H. 1945.** On the use of matrices in certain population mathematics. *Biometrika* 33:183-212.
- Leslie, P. H. 1948.** Some further notes on the use of matrices in population mathematics. *Biometrika* 35:213-245.
- Lint, J. Pers. comm.** BLM, Roseburg, Oreg.
- Lotka, A. J. 1956.** Elements of mathematical biology. Dover, New York.
- Meslow, E. C. Pers. comm.** FWS, Oreg. State Univ., Corvallis.
- Noon, B. R. Pers. Comm.** FS, PSW, Arcata, Calif.
- Noon, B.R., and C.M. Biles. 1990.** The mathematical demography of the spotted owl in the Pacific northwest. *J. Wildl. Manage.* 54:18-27.
- Paton, P. W. C. Pers. comm.** FS, PSW, Arcata, Calif.
- Paton, P. W. C., C. J. Zabel, N. G. Tilghman, and B. R. Noon. Unpubl.** Effects of radio tags on spotted owls. Manuscript in preparation.
- Seber, G. A. F. 1965.** A note on the multiple recapture census. *Biometrika* 52:249-259.
- Southern, H.N. 1970.** The natural control of a population of tawny owls (*Strix aluco*). *J. Zool. London* 162:197-285.

Population Simulation Models

Introduction

Previous analyses of the demography of the spotted owl (Lande 1988, Noon and Biles 1990) have suggested that variation in the age-specific survival rates, and particularly changes in adult survival, strongly affect population growth. Therefore, exploring those factors that strongly affect the survival rates of all age-classes is essential. As territories become more patchy in their distribution because of habitat loss and fragmentation, we predict the likelihood of successful dispersal to suitable habitat areas will decrease. Failure to successfully locate and colonize suitable habitat will be an additional source of mortality for all age-classes. We believe the population dynamics of the owls are complicated by factors associated with habitat loss and fragmentation. These factors include difficulties in finding both mates and suitable territories, changes in prey density and distribution, and increased dispersal mortality from increases in search time. We believe that our model structure captures some of this reality, and that our simulation results demonstrate the significance of these effects to the long-term viability of the northern spotted owl.

We discuss results from two simulation models with different structure. In the first, we explored the dynamics of a two-sex, single-territory (home-range) model and the effects that different magnitudes of suitable habitat loss had in the context of varying dispersal capabilities (Lamberson et al. 1989). This model was developed to crudely approximate the current management design for spotted owl viability: that is, single-pair spotted owl habitat areas (SOHAs) and small territory clusters dispersed across the landscape at specified distances (USDA 1988). Our purpose in developing this model was to explore very general system properties in an attempt to gain insights into what aspects of the species' life-history and behavior most influence its long-term population dynamics.

In a second, single-sex model (Lamberson et al. 1989), we allowed female (pair) territories to be adjacent to each other in clusters of various sizes. The primary goal of this modeling effort was to specifically investigate the advantages of territory clusters of various sizes relative to the single and small-cluster territory pattern of the current management plan (USDA 1988). In this model, we assumed—like Doak (1989)—that successful dispersal within a cluster was more likely than between clusters. This difference arose because of the “resistance” to successful dispersal that occurred within the landscape matrix.

Clarifying the role that computer simulation models, and the inferences drawn from them, played in developing our conservation plan is important. Their role was secondary. Our primary guidance derived from the results of empirical studies of the spotted owl's ecology and life history. The models provided one means of synthesizing this information and suggested aspects of the animal's life history and behavior that may most affect its long-term population dynamics. We sought confirmation of model results from empirical studies of the spotted owl or other

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vertebrate species, and from the predictions of theoretical models (see discussion in appendices N, O, and P). A necessary caution is that the quantitative results of our models should only be interpreted as general qualitative guidelines; they should not be interpreted literally. We have used insights provided by our models as a way of ranking, from most to least important, the many factors that influence the species' population dynamics. Our models, like most, are also a great simplification of all the factors that influence the dynamics of "real" spotted owls.

The Individual-Territory Model

Model Description

In the individual-territory model, we assumed that all newly fledged juveniles dispersed even though a low probability exists that some juveniles may inherit their natal territory. In addition, adult birds (≥ 1 year old) that experienced loss of their territory (from timber harvest) also dispersed. The model focused on a landscape of fixed spatial extent and contained a fixed number of potential home-range territories (or "sites"). Only a fraction of these sites, however, could be occupied (meaning, in a probabilistic sense, that they allowed survival, mate attraction, and reproductive success)—namely those that were stocked by suitable habitat.

The state variables in the model, which were updated annually, were:

- The number T of currently suitable sites (which may be decreasing over time from timber harvest);
- The number P of suitable sites that are occupied by nesting pairs; and
- The number S of suitable sites that are occupied by single males.

A nesting pair annually produced young (according to either some deterministic likelihood or stochastically fluctuating fecundity). These young would disperse at the end of the season, the males seeking an unoccupied site and the females seeking a site occupied by a solitary male. Our simulated landscape can be envisioned as a grid composed of 1000 cells or sites. Each site is either suitable for a territory or unsuitable. Search capability was expressed as the percentage of the landscape that could be searched before the owl died. The likelihood of successful search was affected by whether we assumed an Allee effect (Allee 1935, 1938). If search efficiency was set at 2%, for example, then up to 20 sites could be searched for a suitable site that was unoccupied (no Allee effect), or occupied by an individual of the opposite sex (Allee effect). Dispersal success was density-dependent and was calculated by assuming random search of accessible sites. Various assumptions can be made about the bird's search efficiency; we expressed this as the number of sites an individual was capable of searching before dying. Search capabilities, together with the occupancy ratio of searched sites, determined the bird's potential for successful dispersal. (This calculation was consistent with Lande [1987].) In our model, we allowed dispersing adult birds and females to search twice the number of sites searched by juvenile males. We believed that adult birds were more effective dispersers than juveniles and assumed that females may bypass a suitable territory unless it is occupied by a single male owl.

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Adult birds (≥ 1 year) were subject to mortality, and adults occupying territories were subject to site disturbance (for example, timber harvest); consequently, some surviving adults were also forced to disperse. Juvenile birds also were subject to mortality; in particular, birds that were unsuccessful in dispersal were assumed to have died. To condense the model, we assumed that the number of male and female solitary owls remained equal, that the single females were retained as a floater population, and that all solitary owls had the same vital rates. This assumption allowed considerable simplification without (at our present state of empirical knowledge) any significant loss of accuracy.

We ran the model under a number of alternative assumptions about the proportion of the landscape that was suitable habitat (specified as T over time), the owl's biology and environment (specifying survival and fecundity parameters and search efficiency), and initial population sizes (specifying S and P at time 0). After we specified the proportion of the landscape considered suitable, this proportion of sites was distributed at random across the landscape. We also varied the amount of environmental stochasticity, primarily through a fluctuating fecundity rate to reflect variability in food supply (for example, small rodents).

Model Parameterization

Model parameters were set based on the demographic studies of Franklin et al. (1990) and values published by Marcot and Holthausen (1987). We assumed an annual adult survival probability of 0.92, juvenile predispersal survival of 0.60, fecundity (number of young fledged per adult female) of 0.66, and a 1:1 sex ratio at birth. Single birds (floaters) were assumed to survive at the estimated annual subadult survival rate of 0.77 (table M1).

Results—Individual-Territory Model

Deterministic Analyses

First, we ran the model deterministically (that is, with no environmental fluctuations), while varying the initial population size (initial S and P being kept in fixed proportion). Owl biology (demographic parameters; table M1) and the proportion of the landscape that was suitable habitat (25%) were held constant.

If the initial population was sufficiently large and the search efficiency was relatively high, the population tended to reach a stable equilibrium (fig. M1), but an initially small population crashed (fig. M1). If search efficiency was low, even very large initial populations crashed (fig. M2).

The stable equilibrium was actually two-dimensional (S^* , P^*), which is shown more clearly in a phase-plane portrait (fig. M3). The curve M shown there is an attracting manifold, so that an initial population (S , P) moves quickly, in two or three generations, to its close vicinity. The curve M contains three equilibria; at (S^* , P^*), (0, 0), and an intermediate, unstable equilibrium at ($S^\#$, $P^\#$). A population on M above ($S^\#$, $P^\#$) is drawn quickly to (S^* , P^*), but one below it moves inevitably to extinction at (0, 0).

Figures M1 to M3 illustrate an Allee effect, the result of diminishing female success in finding a mate as the population becomes smaller and more dispersed. Note that, in this two-sex model, the Allee effect arose from an explicit nonlinear mating search-success probability function. Alternative hypotheses on search and the Allee effect are explored by Dennis (1989).

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Table M1—Estimates of parameter values for spotted owl life history used in the model simulations

Parameter	Estimate	Source
s'_0 = fledgling survival probability (predispersal)	0.60	Marcot & Holthausen (1987)
s_d = juvenile probability of successful dispersal	0.18	Marcot & Holthausen (1987)
s_1 = subadult annual survival probability	0.77	Franklin et al. (1988)
s = adult annual survival probability	0.92 ^a	Franklin et al. (1988)
b = adult female average annual fecundity	0.33	Franklin et al. (1988)
a = age at first breeding	2 yrs.	Noon & Biles (1990)
h = current percentage of landscape suitable for spotted owls	32.5% ^b	U.S. Forest Service (1990)

^a This estimate is higher than that reported in Franklin et al. (1990). They report adult female survival rate = 0.90.

^b This estimate is based on the proportion of the forested landscape estimated as suitable spotted owl habitat on National Forest lands in Oregon and Washington.

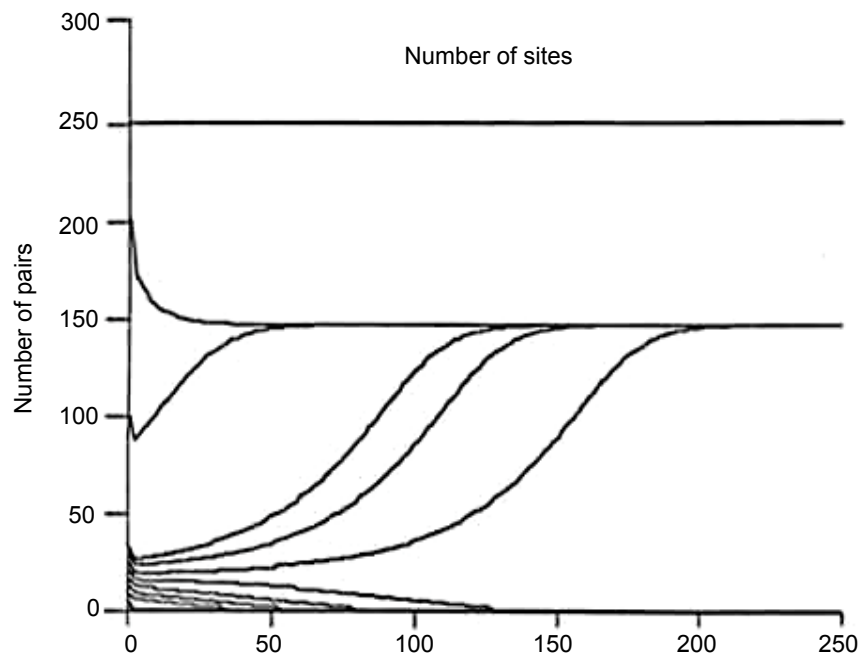


Figure M1—Trend in number of pairs of spotted owls based on a 250-year simulation. Each curve was initialized at a different population size. We assumed that 25% of the landscape was suitable owl habitat, and that juvenile owls could search 3% of the landscape.

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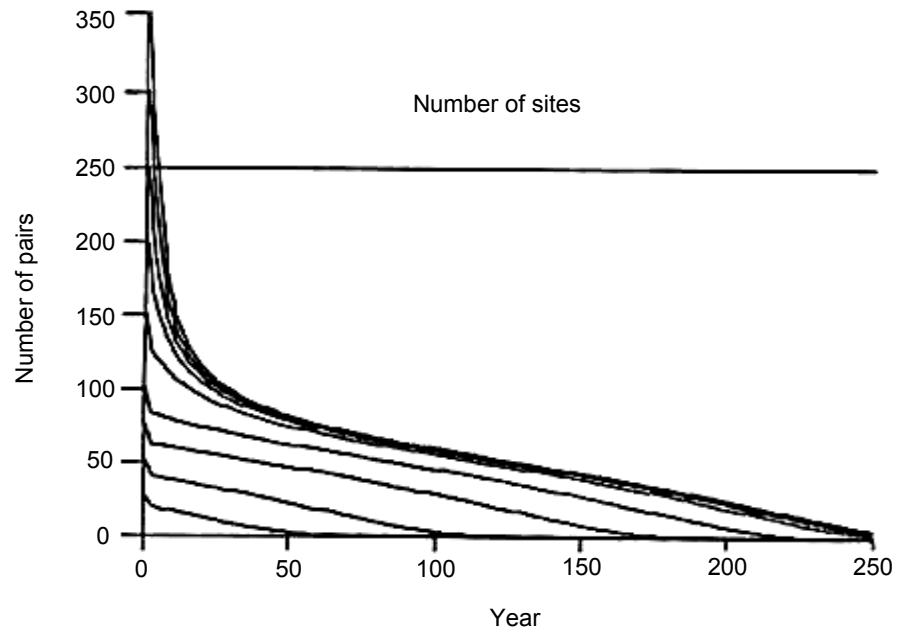


Figure M2—Trend in number of pairs of spotted owls based on a 250-year simulation. Each curve was initialized at a different population size. We assumed that 25% of the landscape was suitable owl habitat, and that juvenile owls could search 1% of the landscape.

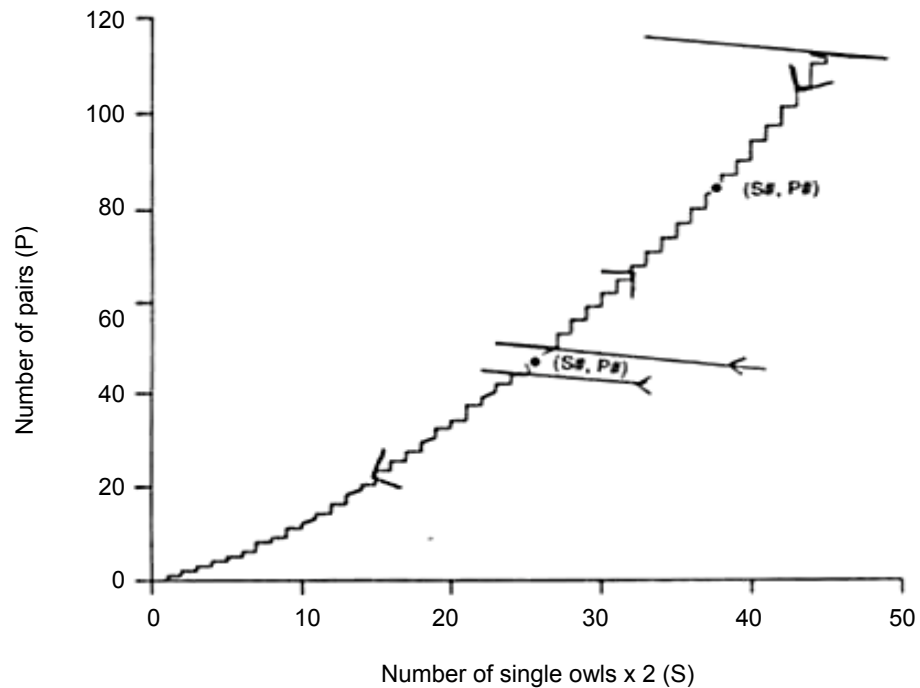


Figure M3—Phase plan of number of pairs of spotted owls against the number of single birds. Stable (S^*, P^*) and unstable $(S^\#, P^\#)$ equilibria points are shown.

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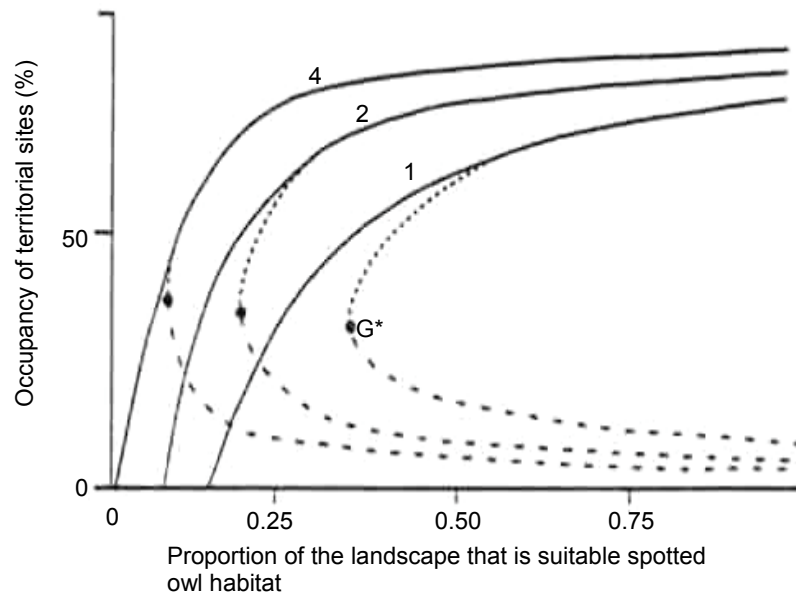


Figure M4—Percentage occupancy of territorial sites (pairs of spotted owls and singles) against the proportion of the landscape that was suitable spotted owl habitat. The solid curve was without an Allee effect. Dotted and dashed curves show a stable and an unstable Allee effect, respectively. Three sets of curves are shown corresponding to various juvenile search abilities (1%, 2%, and 4%).

The locations of the stable and unstable equilibria will depend on the quality of the habitat, as measured by the fraction that is suitable. This dependence is depicted in figure M4 (note that the vertical axis is total occupancy $(S + P)/T$). The various curves correspond to alternative assumptions about the owl's search efficiency (that is, of the maximum percentage of the forest that juvenile males can search before death; fig. M4). The solid line represents the case where every successfully dispersing male is automatically given a mate (no Allee effect). The dotted and dashed curves represent the case where females must search for a mate. On each curve, the solid and dotted lines show the stable equilibrium, and the dashed line indicates the unstable equilibrium. At the left of each curve, the dotted and dashed lines meet at a point (G) that has a specific value for the proportion of the landscape that is suitable habitat (G). For $G < G^*$, the two nontrivial equilibria have disappeared; only the $(0, 0)$ equilibrium remains. Thus for $G < G^*$ all populations become extinct, regardless of initial populations.

Although Lande obtained his result quite differently, our figure M4 is qualitatively the same as his equilibrium configuration (Lande 1987:629). Lande's result was based on a numerical analysis, including density-dependent juvenile survival, and then solved by linearizing locally around the steady-state (Lande, pers. comm.).

Stochastic Analyses

Understanding how environmental stochasticity affects the deterministic patterns is important. Figure M5 shows a few sample realizations of the process, as well as the mean and standard deviation bars for a larger number of runs. To summarize the output of the simulation, we kept track of the fraction of sample runs that led to extinction within a fixed time span.

The probability p of population survival for 250 years as a function of initial population size was expressed as a percentage of suitable sites occupied (fig. M6). The three curves correspond to the three alternative assumptions about environmental stochasticity. With no stochasticity, p is a staircase function, rising abruptly from 0 to 1 at the unstable equilibria of figures M1 to M3.

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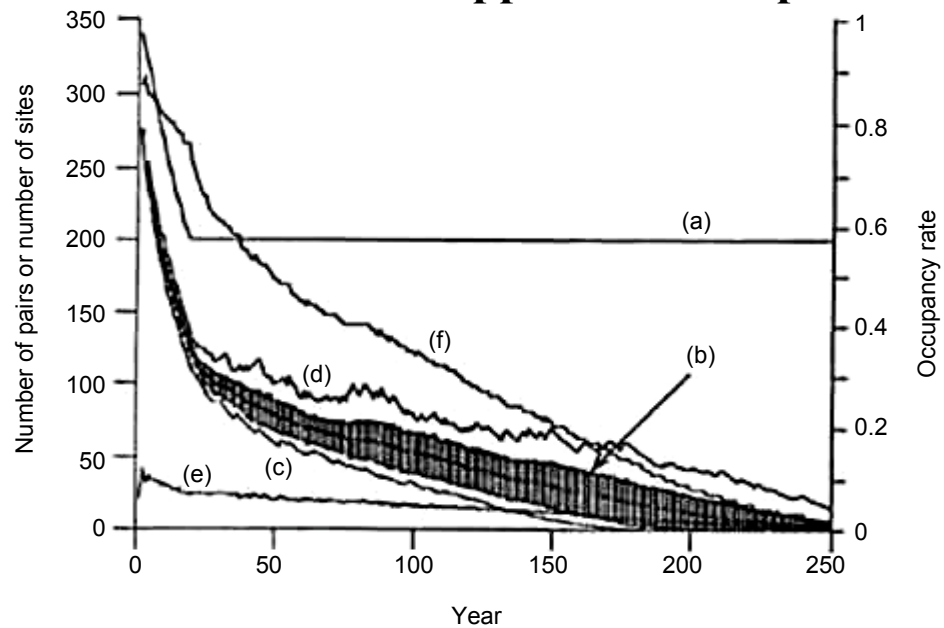


Figure M5—Trends in suitable sites (a), mean number of pairs of spotted owls (b), and mean site occupancy (f) based on 100 250-year simulations. Suitable habitat was lost at the rate of 4% per year until 20% of the landscape remained suitable spotted owl habitat. Juvenile birds were able to search 2% of the landscape. Also shown are the minimum (c) and maximum (d) number of pairs and the number of single birds (e).

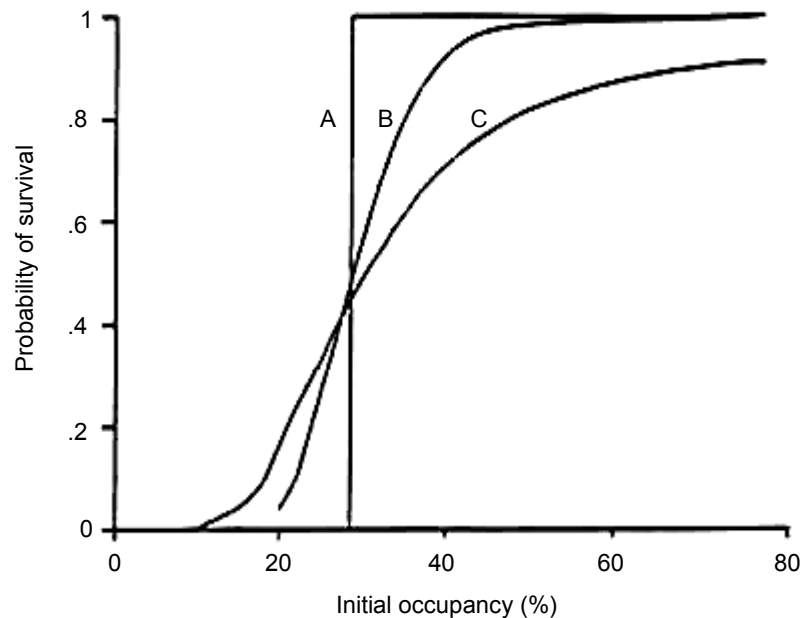


Figure M6—The 250-year survival probability against the initial percentage of the sites occupied by pairs of spotted owls. Curves are shown for three conditions: no (A), low (B), and high (C) environmental variance. We assumed 18% of the landscape was suitable habitat and that adults could search 40 sites (juveniles could search 20 sites).

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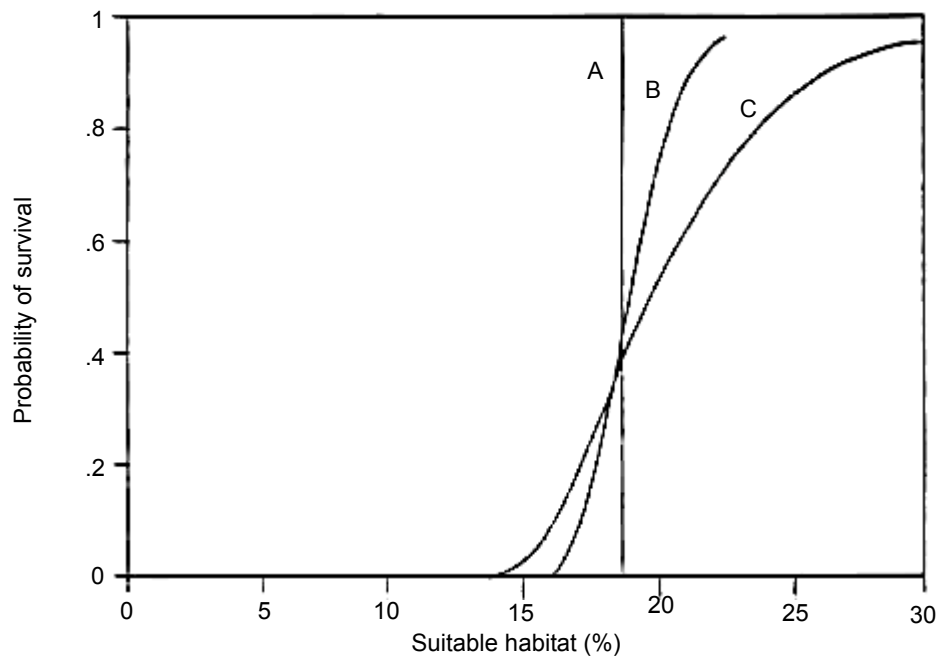


Figure M7—The 250-year survival probability against the percentage of the landscape that was suitable habitat. Curves are shown for three conditions: no (A), low (B), and high (C) environmental variance. We assumed adults owls could search 26 sites (juveniles, 13 sites). All simulations were initialized with the same number of spotted owls.

Adding environmental stochasticity smoothed out the stairstep, as the other two curves, for low and high environmental variance show. Note that for a given **high** probability p , an increase in environmental variance increased the initial occupancy needed to guarantee p ; for a given **low** probability p , an increase in variance decreased the needed initial occupancy. Thus, increasing environmental variance broadened the band of occupancy across which p rose from 0 to 1: that is, the extinction threshold became less abrupt.

Next, we examined the dependence of the probability of survival on the percentage of the landscape that was suitable habitat (G), as manifested in the presence of environmental stochasticity. We computed the 250-year survival probability p as a function of G (fig. M7). Once again, the deterministic case showed a stairstep function, with the jump from 0 to 1 occurring at the point G^* (fig. M4). As before, adding environmental variance smoothed out the stairstep. If a high p (for example, 90% probability of survival for 250 years) is demanded, then the greater the environmental variance, the higher the proportion of suitable habitat required to guarantee it. On the other hand, greater environmental variance also means a less abrupt threshold into the high-risk zone.

We explored the sensitivity of these results to our model assumptions, both biological and environmental (fig. M8). The various curves illustrate the 250-year survival probability p under a variety of assumptions of search capability and environmental variance. Note that the threshold into the high-risk zone was always quite steep, indicating an extreme sensitivity to the amount of habitat in the landscape that remained suitable at a given point in time. Increasing the owl's dispersal capabilities shifted the threshold to the left but did not change its abruptness (fig. M8).

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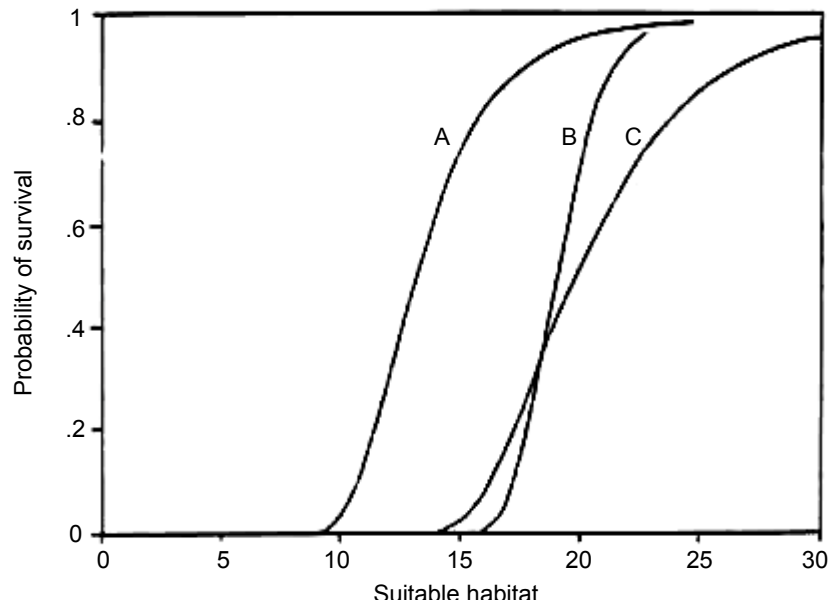


Figure M8—The 250-year survival probability against the percentage of the landscape that was suitable habitat. Curves are shown for three conditions: low environmental variance, 26 sites searched (B); and high environmental variance, 40 (A) and 26 (C) sites searched. Search refers to adult spotted owls (juvenile search is half adult search). All simulations were initialized with the same number of owls.

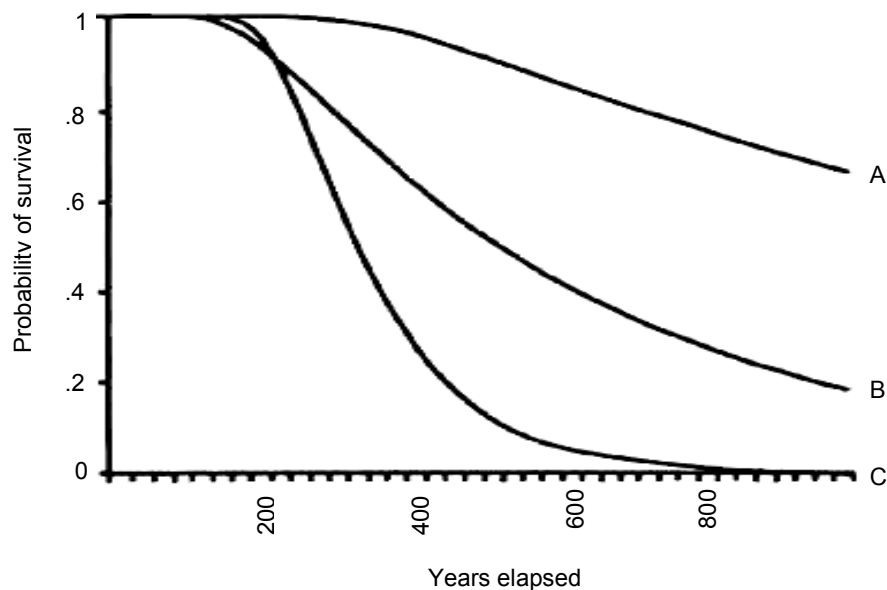


Figure M9—Probability of survival against years elapsed. Curves are shown for three conditions: 27% suitable habitat and (A) low and (B) high environmental variance, and (C) 21.5% suitable habitat and low environmental variance. All simulations were initialized with the same number of spotted owls.

For specified amounts of suitable habitat and environmental variance, we computed the population survival probability p as a function of time (fig. M9). Survival to 250 years was but a single point on each of these curves; implying that this single statistic carries very incomplete information about the viability of a stochastically driven population.

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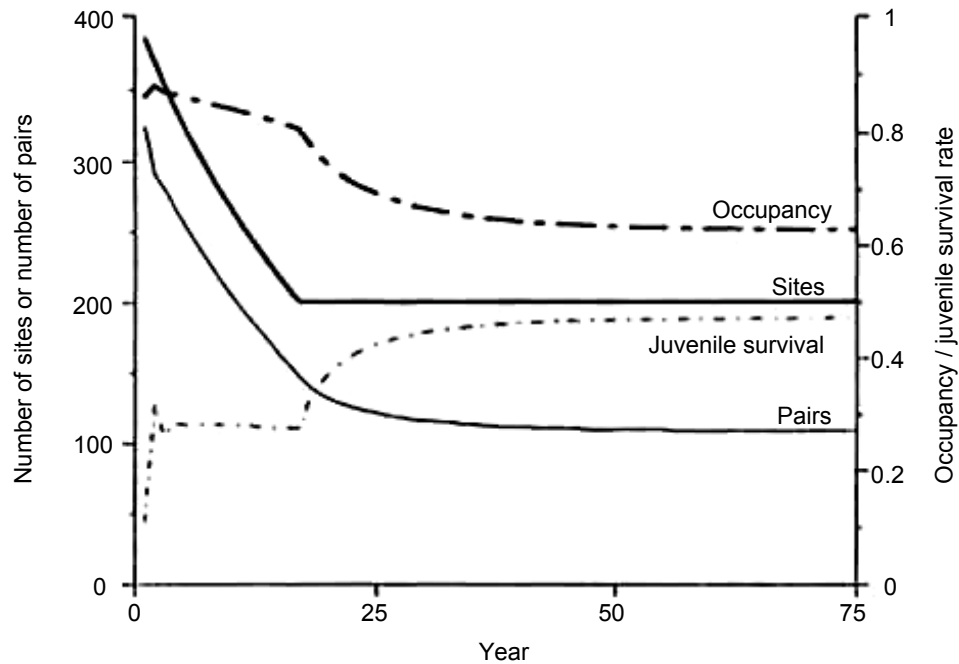


Figure M10—Trend in number of pairs of spotted owls, number of sites, site occupancy by pairs, and juvenile survival rate based on a 75-year simulation. We assumed that 4% of the suitable owl habitat was lost per year until 20% remained, and that juvenile owls could search 2% of the landscape.

Introducing Landscape Dynamics

We examined the model both deterministically and stochastically but allowed the proportion of the landscape that was suitable spotted owl habitat to be diminished (for example, by fire or timber harvest). Thus, for the first time, the dynamic nature of the landscape was entered into model simulations. We plotted the proportion of the landscape that remained as suitable habitat, T , as a function of time (fig. M10). We assumed that suitable owl habitat was being lost at a rate of 4% of the remainder per year (that is, through timber harvest) until 20% of the landscape remained as suitable habitat. At this point, no further loss of suitable habitat took place. Simultaneously, we tracked the occupancy of the suitable habitat (number of sites occupied by pairs; P/T).

Note that site occupancy remained virtually unchanged during the period when habitat loss was occurring (fig. M10) as a consequence of a population crowding effect. The owls that initially held territories found them when the amount of suitable habitat was greater and, as a result, unoccupied sites were easier to locate. As suitable habitat continued to decline (that is, from timber harvest), the amount of suitable habitat was reduced; at the same time, some adult pairs of owls were displaced from their territories. Displaced adults were in competition with dispersing juveniles for the remaining, smaller amount of suitable habitat. The juveniles in our model (and probably in reality) were less likely than adults to be successful in their search for a suitable territory. Thus, the remaining suitable habitat was more densely occupied than we would expect at equilibrium. Further, suitable habitat was highly occupied by owls that were, on the average, older than expected from an equilibrium population. Simultaneously, we observed unusually low juvenile survival rates because of the difficulty juveniles had in finding suitable, unoccupied territories (fig. M10).

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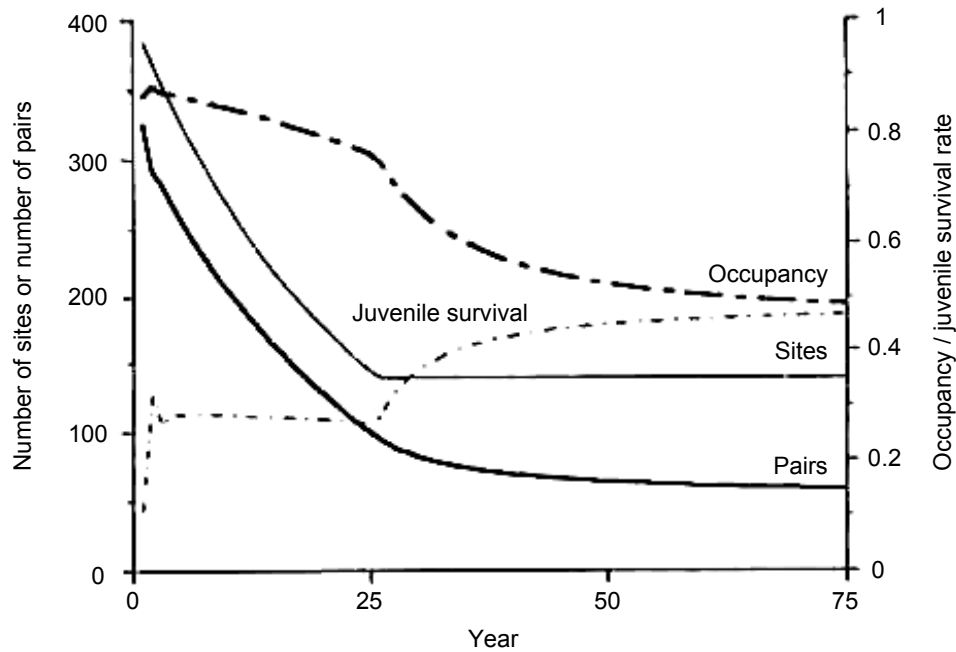


Figure M11—Trend in number of pairs of spotted owls, number of sites, site occupancy by pairs, and juvenile survival rate based on a 75-year simulation. We assumed that 4% of the suitable owl habitat was lost per year until 4% remained, and that juvenile owls could search 2% of the landscape.

As the population passed beyond the period of declining suitable habitat, it eventually came into equilibrium with a landscape that contained less—and more dispersed—suitable habitat. Even after suitable habitat was no longer being lost, the population continued to decline for several generations. Gradually, the population age-structure assumed a more stable distribution, less dominated by older owls. At the same time, the juvenile survival rate increased because of decreased competition for unoccupied, suitable sites. This increase occurred because logging was no longer displacing adult owls, and because new territories were becoming available as adult birds died.

Given both an adequate initial population size and final amount of suitable habitat, the model reached an equilibrium (fig. M10). The equilibrium population was substantially smaller than observed during the period of habitat loss. Note however, that this population, if assessed only by occupancy, would have appeared relatively stable for the first 20 years. We believe that assessing population trends from data collected during periods of declining carrying capacity (for example, the harvest of suitable owl habitat) may be very difficult because of the difficulty of distinguishing a collapsing population (fig. M11) from one that eventually reaches a long-term stable equilibrium (fig. M10). Recall that our most reliable estimates of the finite rate of population change (λ) have been made from populations in areas that were experiencing loss of suitable habitat (see appendix L).

Environmental uncertainty, coupled with habitat loss, was simulated through stochastic fecundity. The trends in population, occupancy, and juvenile survival were similar in the stochastic version of the model to that previously discussed (compare fig. M10 with fig. M12).

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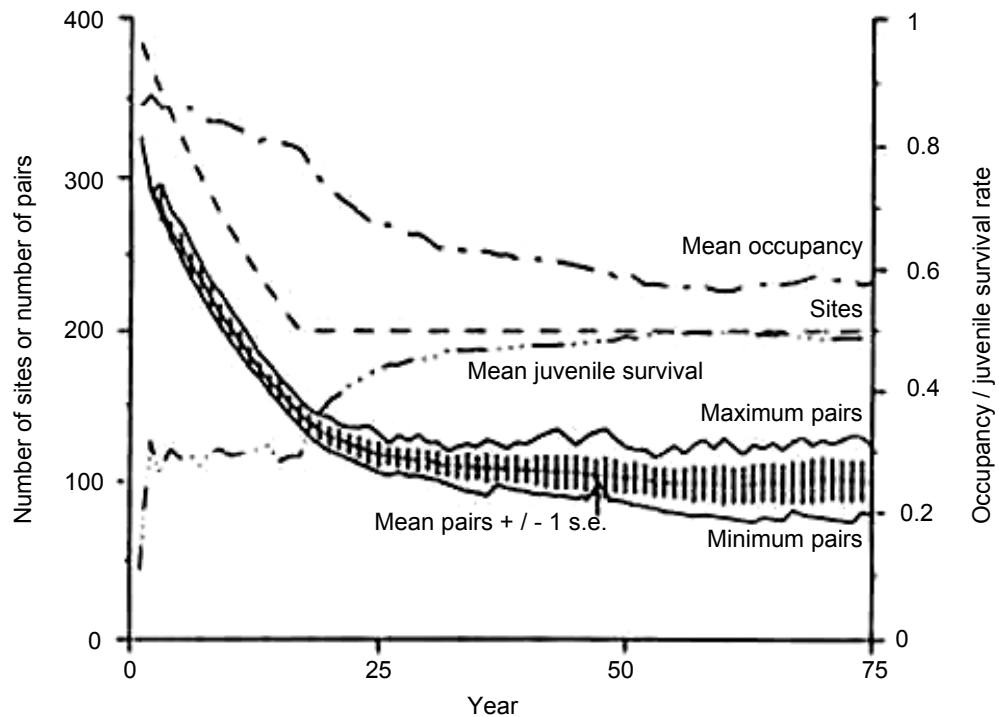


Figure M12—Trend in number of pairs of spotted owls, number of sites, site occupancy by pairs, and juvenile survival rate based on a 75-year stochastic simulation. We assumed that 4% of the suitable owl habitat was lost per year until 20% remained, and that juvenile owls could search 2% of the landscape.

Introducing a Secondary Habitat Type

To introduce a population of owls that occupied secondary habitat, we assumed that all dispersing juvenile owls that were unsuccessful in their search for a suitable territory in primary habitat entered a secondary habitat. The survival rate for this population was arbitrarily chosen to be 0.6. These owls were assumed to search each year for a site in primary habitat. If they failed to find a suitable territory they returned to the secondary population. The model provided for reproduction in this population at a rate that was 30% of the rate in primary habitat.

During the period of ongoing habitat loss, the population that occupied secondary habitat was a measurable fraction of the total population. As habitat loss ceased, however, this population gradually shifted to primary habitat and, in the long term, became only a minor part of the total (fig. M13). The contribution of the secondary population was to provide a source of owls to occupy sites that became available during the restructuring of the population subsequent to the end of habitat loss. As a result, the length of the long-term decline in the population was extended, as was the “bump” in the occupancy curve. The presence of secondary habitat may also have slightly lowered the extinction likelihood resulting from habitat loss. We need to investigate this possibility further but, at this time, believe that the effects of secondary habitats are relatively small.

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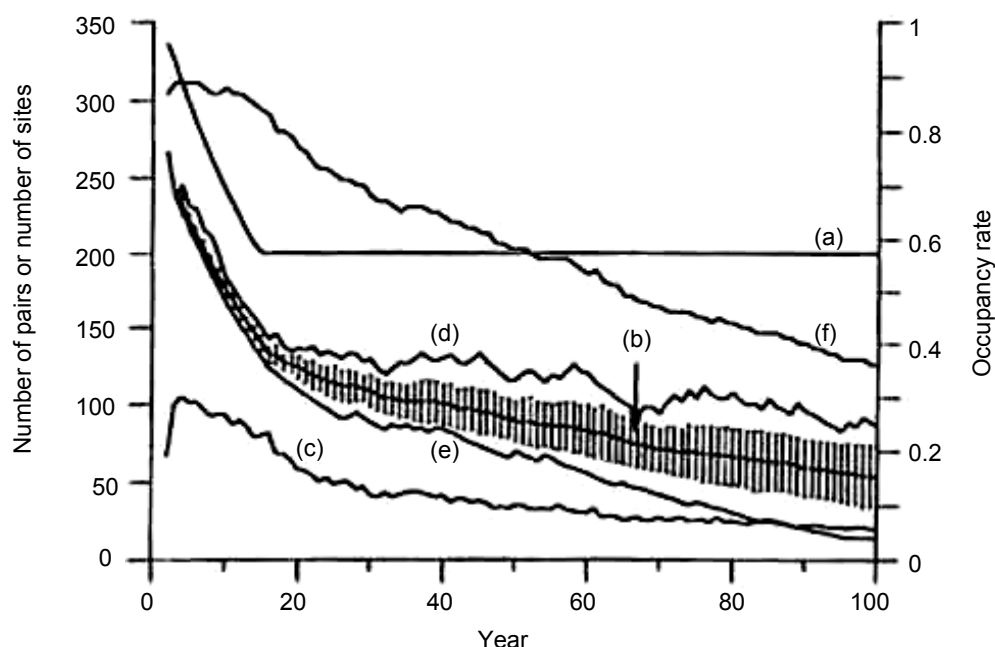


Figure M13—Trend in number of pairs of spotted owls in primary (b) and secondary (c) habitat, number of sites (a), and site occupancy by pairs (f), based on a 100-year stochastic simulation. We assumed that 4% of the suitable owl habitat was lost per year until 20% remained, and that juvenile owls could search 2% of the landscape. Also shown are the minimum (e) and maximum (d) number of pairs.

Edge Effects

We have done some preliminary analyses of edge effects. Edge effects were introduced into the model by allocating some of the search time of juveniles, originating from sites adjacent to edge, to be in unsuitable habitat beyond the edge. In general, edge effects reduced the viability of the population. The reduction was small for our simulated landscape with 1000 suitable sites and a minimum of edge, but the edge effect may be important for highly fragmented landscapes with irregular-shaped polygons of suitable habitat imbedded in a landscape matrix of high contrast. In this scenario, edges may act as partial or total absorbing boundaries and significantly contribute to the annual mortality rate. We plan to explore the significance of edges in considerably more detail.

Discussion— Individual—Territory Model

Several models have investigated the population dynamics of spotted owls. The most detailed one was developed as part of the original FS spotted owl viability analysis, and is described in detail in the FSEIS (USDA 1988; see also Marcot and Holthausen 1987). That analysis used a linear, single-sex, Leslie matrix model, which has been criticized (Boyce 1987), in part because its linear structure caused it to display unrealistic, stochastic output. Our most direct comparison with the linear model is displayed in our phase-plane portrait (fig. M3). For a linear model, the attracting manifold M would be a straight line, with the coordinates of a representative point being in stable-age proportion. An initial population would move to M (how quickly would depend on the degree of dominance of the leading eigenvalue, λ , the implicit growth rate). The population then would grow geometrically (if $\lambda > 1$) or collapse to the origin (if $\lambda < 1$). Only for $\lambda = 1$ would the population remain stable.

In our model, the presence of nonlinear search success effectively made λ density dependent (with the corresponding age distribution also density dependent). Also, $\lambda = 1$ only at the stable and unstable equilibria, and $\lambda > 1$ only above the latter.

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Our search functions are patterned after a second model, that of Lande (1987), and our deterministic equilibrium configuration (fig. M4) is equivalent to his result. Because his model prescribed only equilibrium behavior, however, it was not well adapted to exploring environmental or demographic stochasticity. (But see equation 17 in Lande 1987:632.) Lande's deterministic analysis can be thought of as leading to the stair-step threshold functions (figs. M6 and M7). (The exact locus of the step-break depends on the assumptions about parameter values.) Thus, the real difference between our results and Lande's was in our treatment of environmental stochasticity and a changing carrying-capacity because of timber harvest.

A third model is that of Boyce (1987). Boyce argued (correctly, we believe) for the need to incorporate density-dependent and spatial effects into any model, and he discussed at some length the Allee effect. He illustrated his ideas through a standard stage-structured, single-sex, Leslie-Lefkovich model (Leslie 1945, 1948; Lefkovich 1965), with survival and fecundity made density dependent. The compensatory fecundity function he chose for his illustration, however, turned out to be too mild for the Allee effect to become operative. When we incorporated into Boyce's model a search-effectiveness function like Lande's (or like ours), we found that the Allee effect was operative, with results consistent with our own.

We believe two major conclusions can be drawn from our modeling efforts. First, two rather sharp thresholds occur, both of which can lead to the ultimate extinction of the population. One results from the loss of habitat: if the amount of suitable habitat is reduced to an excessively small fraction of the landscape, then the difficulty in finding a suitable territory becomes an insurmountable barrier to the population. The second threshold is due to the Allee effect: if the population numbers fall too low, then the probability of finding a mate drops below that required to maintain the reproductive rates necessary to support a stable population. Both of these results indicate that a species can be severely habitat limited even in the presence of suitable, but unoccupied habitat.

Second, the fact that we are modeling a dynamically changing system critically affects our analysis and results. The crowding of older owls into the remaining suitable habitat as a consequence of habitat loss is likely to produce high occupancy rates—much higher than expected under long-term equilibrium conditions (no decline in carrying capacity). Equilibrium occupancy rates are well below those observed while loss of suitable owl habitat is continuing. As a result, we suggest care when drawing inferences to long-term abundance or population trend from short-term occupancy. To illustrate, figure M11 shows that occupancy during the habitat-loss phase remains virtually unchanged, but the population ultimately crashes, long after habitat loss has ceased. Assuming our model results are reliable, they suggest that the current FS monitoring program, based on SOHA occupancy rates, may be slow to reflect even substantial population declines.

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The juvenile survival rate was substantially depressed during the habitat loss phase, but it increased after suitable habitat was no longer being lost (figs. M10 to M12). This habitat effect, a consequence of competition between juvenile and adult birds for access to available sites, may partially explain the very low estimates of the 1st-year survival rates computed from field studies (Franklin et al. 1990; Forsman, pers. comm.). For a population experiencing a decline in its carrying capacity, a habitat-mediated reduction in 1st-year survival rate would contribute to a long-term growth rate (λ) that is <1.0 .

Our simulations may appear overly optimistic about the long-term survival of the spotted owl. The long-term growth rate of the population is an order of magnitude more sensitive to variation in adult survival rate than to other demographic parameters (Lande 1988, Noon and Biles 1990), and our simulations used a higher estimate of adult survival rate ($s = 0.92$). The most current estimate of adult female survivorship is 0.90 (Franklin, pers. comm.).

Our individual-territory model provided some important, general insights and suggests the wisdom of proceeding cautiously in making management decisions that affect spotted owl habitat. Some sharp population threshold points are likely which, once passed, could lead to the local extinction of owl populations. At the same time, none of our numbers should be taken as exact measures of where these threshold points lie. Our model is of sufficient sophistication to examine the system and discover the existence of threshold points. Our knowledge of the model structure and of spotted owl dispersal and search capabilities is incomplete, however, and we cannot accurately predict the population size, suitable habitat, or amount of habitat fragmentation thresholds that, once crossed, would lead to a population crash.

Territory-Cluster Model

Model Description

The basis of the territory-cluster model was a continuous, rectangular array of potential owl habitat clusters. The usual assumption was that these clusters comprised 35% of the total landscape. We assumed the clusters to be circular and every owl site (territory) within a cluster was considered to be of identical size (for example, 3000 acres). The matrix between clusters was assumed to be entirely unsuitable for owl territories, and the clusters were either partially or totally suitable. Thus, a cluster was a collection of sites. All sites, or only a subset of the sites, within a cluster were considered capable of supporting pairs. The carrying-capacity of a cluster was equal to its number of suitable sites.

The territory-cluster model was an all-female stage projection model with the stage-classes being juveniles, subadults, and adults. This structure was similar to that of Boyce (1987) and Lande (1987, 1988). Fecundity in this model was stochastic and varied to represent good and bad years for reproduction. We assumed a fecundity of 0.25 female young per adult female in bad years (75% of the time) and 0.50 in good years (25% of the time). These values and year-type probabilities gave a deterministic fecundity, 0.33, equal to that estimated from the data (table M1).

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Each cluster was composed of an assigned number of sites (territories) with a given number (or percentage) of them considered suitable habitat. The carrying capacity of a cluster, measured in terms of female owls (≥ 1 year old), or owl pairs, was the total number of suitable sites in that cluster. Within each cluster, owl numbers were stored in a numerical array in terms of adults (≥ 2 years old), subadults ($1 \leq \text{age} < 2$ years), and postdispersal juveniles ($0 < \text{age} < 1$ year). The total for a cluster was never allowed to exceed the carrying capacity of that cluster.

Before dispersal, the number of juvenile owls was reduced by predispersal mortality (table M1). These deaths were assigned at random to juvenile owls throughout the array of clusters.

The model distinguished between dispersal within a cluster and dispersal between clusters (compare Doak 1989). The dispersal within a cluster followed Lande (1987), with each dispersing owl allowed to sample with replacement a given number, m , of sites within the cluster. The probability of successful dispersal within the cluster was computed as 1 minus the probability of failing to find a suitable, unoccupied site within the given number of trials,

$$\text{prob}(\text{success}) = 1 - [1 - \# \text{ available sites} / \text{total} \# \text{ sites}]^m. \quad (1)$$

No further mortality was assigned to juveniles that succeeded in finding a site within their natal cluster.

If the juvenile female owl did not succeed in finding a territory within her natal cluster, she was forced to disperse between clusters. When the owls dispersed from their natal cluster, two sources of mortality existed. First, the juvenile female may have gone in a direction that failed to intercept an adjacent cluster (the direction of dispersal, within a specified search angle, was chosen at random). As an example, when clusters each contained 10 sites and accounted for 35% of the landscape, juvenile mortality from this source occurred about 22% of the time. Second, given the selection of an appropriate direction, the likelihood of successful dispersal was modeled by a decaying exponential,

$$\exp(-k * \text{distance between clusters in km}). \quad (2)$$

Based on an average cluster size of 10 sites, when $k = 0.1$, about 58% of juveniles that chose the correct direction successfully arrived at the nearest, adjacent cluster, about 5.6 km (3.5 miles) away, the distance to the four nearest clusters when 35% of the landscape was in clusters. With $k = 0.3$, about 20% were successful, and for $k = 0.03$, over 85% were successful.

Appendix M: Population Models

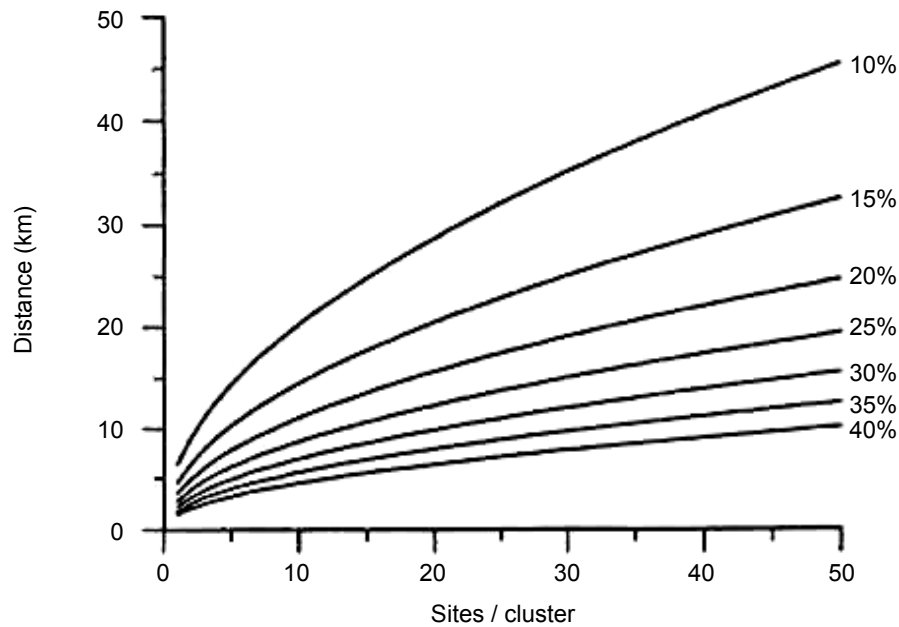


Figure M14—Nearest neighbor distance between clusters against cluster size. Each curve represents a different percentage of the landscape assumed to be suitable spotted owl habitat and located within the clusters.

Assuming that a constant percentage of the landscape was potentially suitable owl habitat, and restricting the habitat to the clusters, had two important consequences. First, as average cluster size increased, the distance between adjacent clusters increased in a predictable way (fig. M14). We believe this consequence accurately reflected real-world constraints encountered in developing a species' conservation strategy. We envision that most conservation plans will reflect a compromise between the size of habitat conservation areas and the distance between them. Second, the dispersal angle and the probability associated with selecting this angle were constant regardless of the average cluster size.

Once a juvenile had successfully traveled to an adjacent cluster, she repeated the within-cluster search process as in the natal cluster (equation 1). The number of clusters that could be searched could be systematically varied. If unsuccessful in the first cluster, travel to an additional cluster(s), was allowed. The likelihood of successful movement between clusters declined exponentially with distance (equation 2). Dispersing owls were chosen in order, and the occupancy data (age distribution) within each cluster were updated after each dispersal.

For the results reported here, the landscape simulated by the model had a “wrap-around” structure and did not include edge effects. The clusters on the right side of the grid were treated within the model just as though they were immediately to the left of those on the left side of the grid. The top and bottom rows of clusters were treated in a similar fashion.

Unless otherwise noted, the model was initialized at 80% of the carrying capacity with the age-structure near that expected at equilibrium (stable age-structure about 20 juvenile : 5 subadult : 75 adult). The owls were distributed to the clusters at random, making sure that none of the clusters exceeded its carrying capacity. All simulations were stochastic with 10 replications per simulation.

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The state variables in the model, which were updated annually after the dispersal events, were:

- The number T of suitable sites within a cluster;
- The number P of suitable sites within a cluster occupied by a female owl (= pair of owls); and
- The proportion of suitable sites O within a cluster occupied by pairs (= P/T).

Setting Model Parameters Parameters of the life-history component of the model were based on the demographic studies of Franklin et al. (1990). We assumed an annual adult survival probability of 0.92, juvenile predispersal survival of 0.60, fecundity (number of young fledged/adult female) of 0.86, and a 1:1 sex ratio at birth. One-year-old birds were assumed to survive at the estimated annual subadult survival rate of 0.77 (table M1).

Results— Territory-Cluster Model The number of model parameters, their range of values, and their possible combinations were immense (table M2). We report on only a small subset of the possible combinations of parameters, in an attempt to portray the sensitivity of the owls' population dynamics to variations in parameter values. In general, we varied the model parameters one at a time, holding all others constant. Variations in some model parameters had little affect on model outcome. Therefore, conditioned on the reality of our model structure, we inferred that they were of little relevance to the owls' population dynamics.

Table M2—Values of model parameters used in the simulations

Parameter	Values
h = fraction of the landscape located within the clusters	0.10, 0.15, 0.20, 0.25, 0.30, 0.35, 0.40
c = cluster size (number of territories/cluster)	5, 7, 10, 15, 20, 25
p = percentage of cluster sites that are suitable	40, 50, 60, 75, 100
m = number of sites searched per cluster	5, 10, 15, 20, 25
k = dispersal coefficient	0.03, 0.1, 0.3, 1.0
Dispersal functions	
Within-cluster dispersal	$\text{Pr}(\text{success}) = 1 - [1 - (\frac{\text{available sites}}{\text{total sites}})]^m$
Between-cluster dispersal	$\text{Pr}(\text{success}) = \exp(-k * \text{distance between clusters})$

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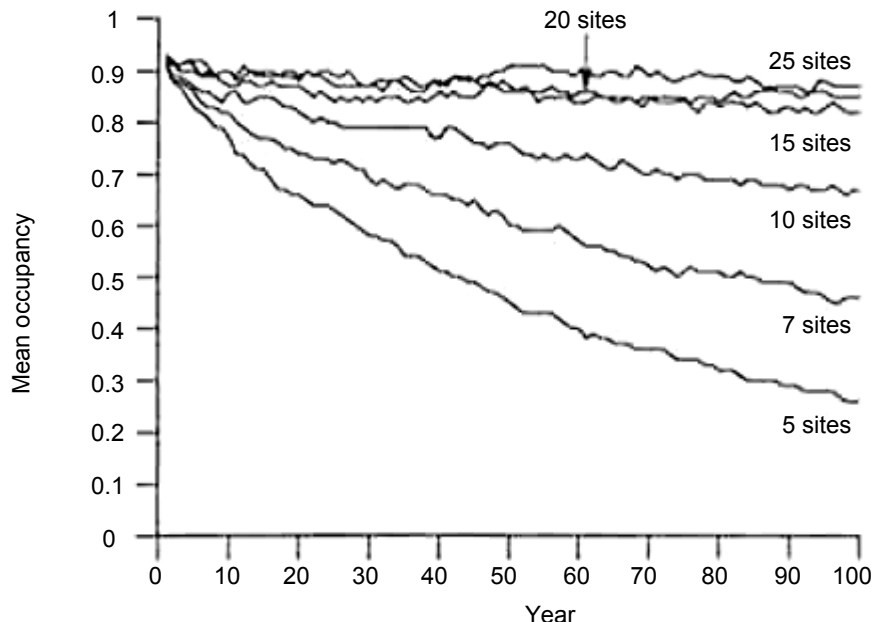


Figure M15—Mean cluster occupancy proportion against time for a 100-year simulation. The number of suitable sites per cluster was varied from 5 to 25. Model parameters (table M2) were: $h=35\%$; $p=100\%$; $m=12$; $k=0.1$.

We varied the number of sites per cluster over a range of values (table M2) and plotted the trend in average pair occupancy per cluster out to 100 years (fig. M15). For this simulation, all sites within a cluster were assumed suitable, 12 sites could be searched per cluster ($m=12$), and the dispersal coefficient equaled 0.1 ($k=0.1$). Recall that when all sites within a cluster were considered suitable, the carrying capacity of the cluster was equal to the number of sites. Given these conditions, we did not observe a stabilization of mean occupancy until at least 15 suitable sites were in each cluster. Below 15 sites per cluster, mean occupancy did not reach an equilibrium other than zero. The occupancy rate in clusters with <7 sites declined rapidly. Once clusters contained 15 suitable sites, however, increasing cluster size had little effect on the equilibrium level of mean occupancy (fig. M15).

At a given point in time, two possible explanations exist for why all sites within a cluster may not be suitable. First, when the clusters, or habitat conservation areas (HCAs), are initially designated, many will not contain sites all of which are suitable. In general, far less than 100% of the potentially suitable sites within a cluster will be suitable at the initiation of the conservation plan. Second, many HCAs will contain one or more sites which can never become suitable. Both these factors result in a maximum HCA carrying capacity that is less than the total number of potential sites within the HCA.

We hypothesized that the cluster size at which mean occupancy would reach an equilibrium would depend on how far clusters were below their potential carrying capacities. To test this hypothesis, we performed a simulation as above except that $<100\%$ of the sites within a cluster were suitable. When $<100\%$ of the sites were suitable, the carrying capacity of a cluster was changed to the number of sites it contained times the percentage suitable. In this simulation, assuming that 60% of the sites were suitable, mean occupancy did not reach an equilibrium until clusters contained ≥ 20 sites (that is, ≥ 12 suitable sites per cluster; fig. M16).

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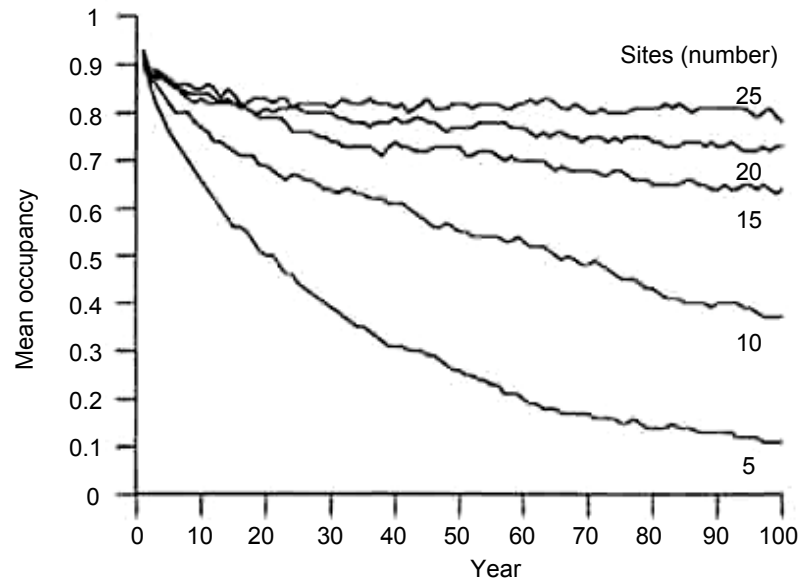


Figure M16—Mean cluster occupancy proportion against time for a 100-year simulation. The number of suitable sites per cluster (cluster size) was varied from 5 to 25. Model parameters (table M2) were: $h = 35\%$; $p = 60\%$; $m = 12$; $k = 0.1$.

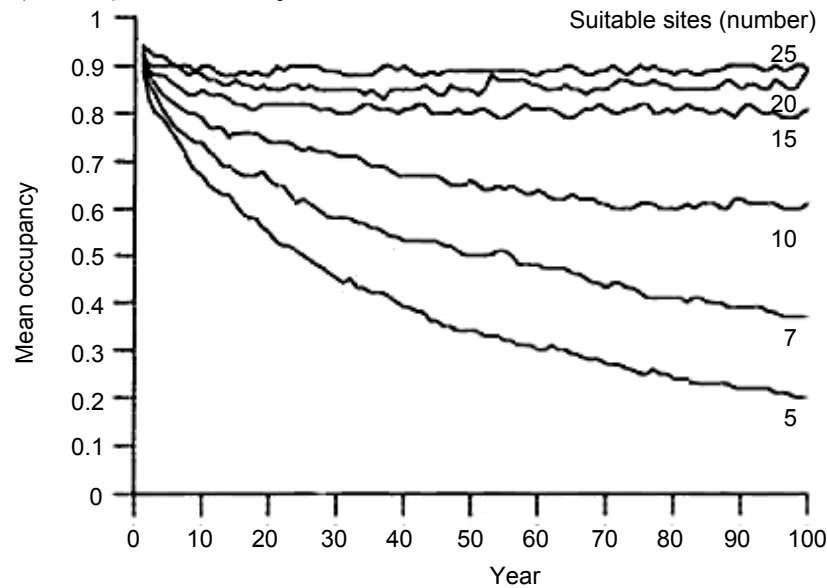


Figure M17—Mean cluster occupancy proportion against time for a 100-year simulation. The number of suitable sites per cluster was varied from 5 to 25. Cluster size was fixed at 25. Model parameters (table M2) were: $h = 35\%$; $c = 25$; $p = 100\%$; $m = 12$; $k = 0.1$.

We explored the effect, on mean occupancy, of clusters being below their potential carrying capacities in another way. We assumed a variable number of suitable sites within clusters, all with a potential carrying capacity of 25 pairs (fig. M17). The proportion of suitable sites within clusters ranged from 0.2 (5/25) to 1.0 (25/25). All other model parameters in this simulation were identical to those in figures M15 and M16. The results suggest that mean occupancy did not stabilize, over the long term, until 40 (10/25 X 100) to 60 (15/25 X 100) percent of the sites within a block were suitable. For smaller HCAs, the percentage of suitable sites required for equilibrium would increase.

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Variation in the percentage of the landscape included within the clusters interacted with both cluster size and the percentage of suitable sites to affect mean occupancy. We investigated the strength of this interaction through a series of simulations. We systematically varied the landscape percentage from 15 to 35%, for three cluster sizes, 5, 10, and 20 sites per cluster. To illustrate the pattern of interaction among these variables, we initially assumed that 60% of the cluster sites were suitable. For a given cluster size, increasing the percentage of the landscape in clusters increased mean occupancy (figs. M18 to M20). The increase, however, was much more dramatic for small clusters (5 or 10 sites) than for large clusters (20 sites; compare fig. M18 with fig. M20). When we increased the percentage of suitable sites from 60 to 100%, the effect of variation in landscape percentage on mean occupancy was much reduced, particularly for clusters of size 20 (figs. M21 to M23).

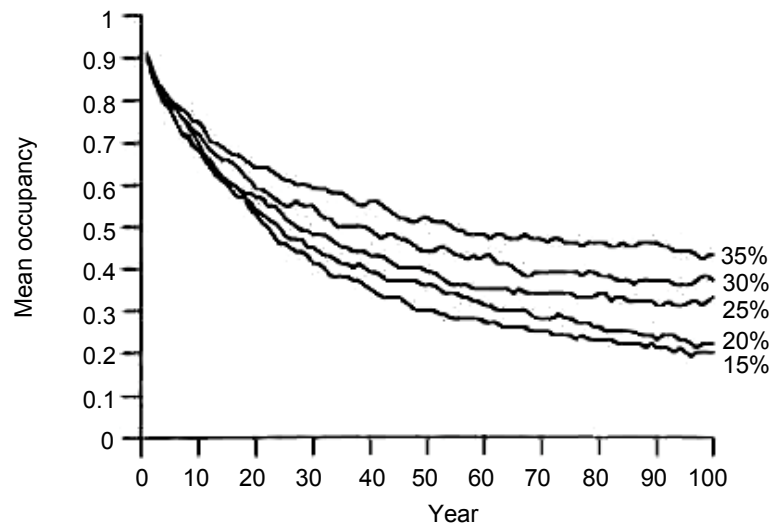


Figure M18—Mean cluster occupancy proportion against time for a 100-year simulation with 15 to 35% of the landscape within the clusters; 5 sites per were in each cluster, of which 60% were suitable. The total number of possible searches was 30. Model parameters (table M2) were: $m = 5$; $k = 0.1$.

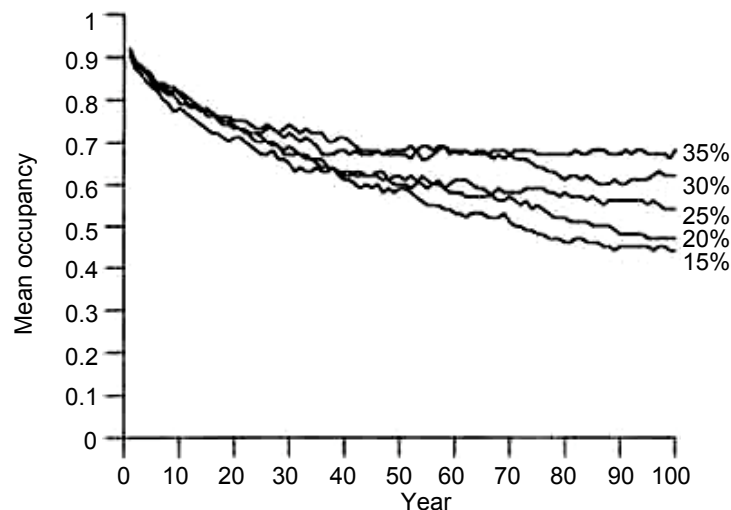


Figure M19—Mean cluster occupancy proportion against time for a 100-year simulation with 15 to 35% of the landscape within the clusters; 10 sites were in each cluster, of which 60% were suitable. The total number of possible searches was 30. Model parameters (table M2) were: $m = 10$; $k = 0.1$.

Appendix M: Population Models

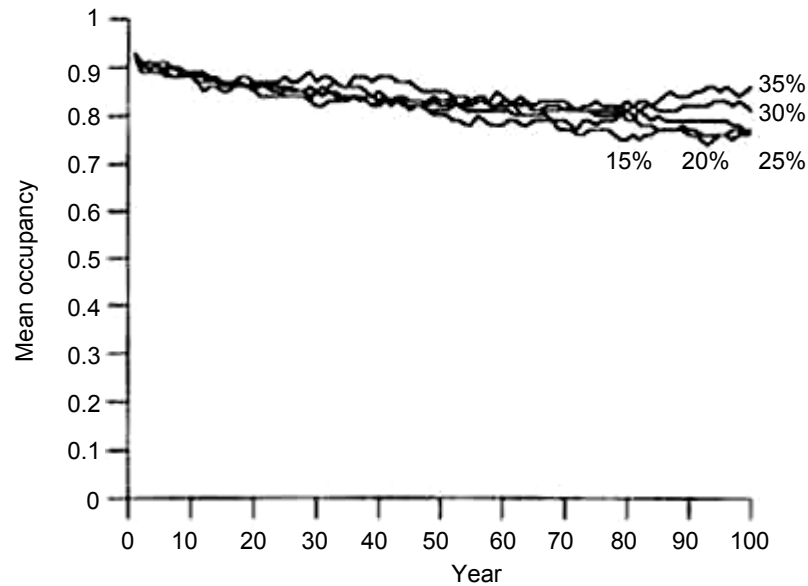


Figure M20—Mean cluster occupancy proportion against time for a 100-year simulation with 15 to 35% of the landscape within the clusters; 20 sites were in each cluster, of which 60% were suitable. The total number of possible searches was 30. Model parameters (table M2) were: $m = 20$; $k = 0.1$.

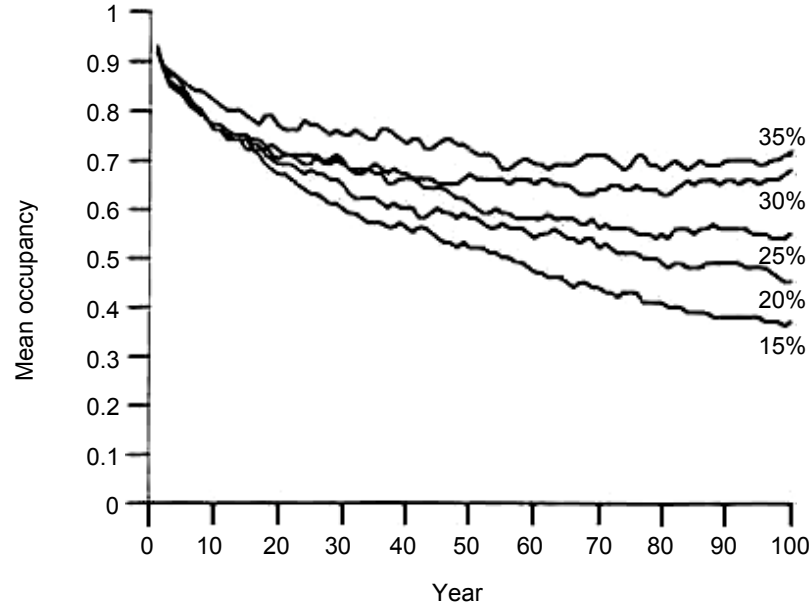


Figure M21—Mean cluster occupancy proportion against time for a 100-year simulation with 15 to 35% of the landscape within the clusters; 5 sites were in each cluster, of which 100% were suitable. The total number of possible searches was 30. Model parameters (table M2) were: $m = 5$; $k = 0.1$.

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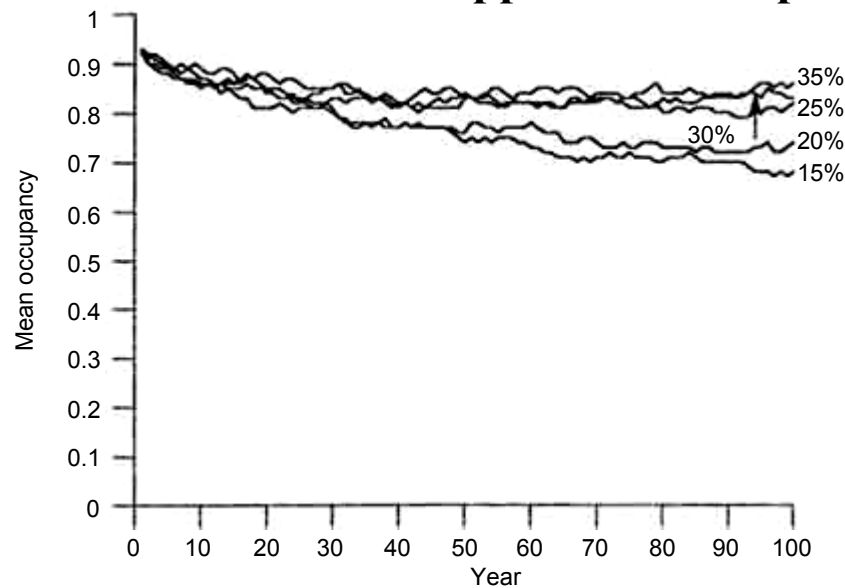


Figure M22—Mean cluster occupancy proportion against time for a 100-year simulation with 15 to 35% of the landscape within the clusters; 10 sites were in each cluster, of which 100% were suitable. The total number of possible searches was 30. Model parameters (table M2) were: $m = 10$; $k = 0.1$.

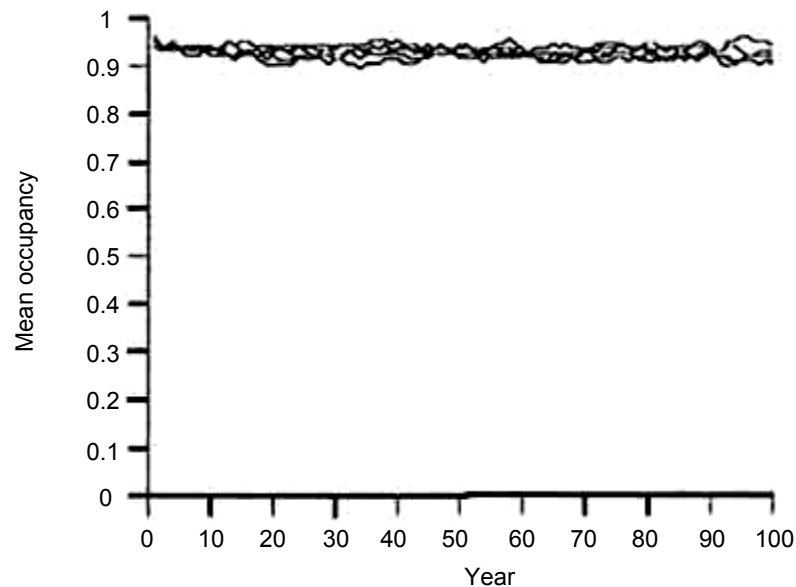


Figure M23—Mean cluster occupancy proportion against time for a 100-year simulation with 15 to 35% of the landscape within the clusters; 20 sites were in each cluster, of which 100% were suitable. The total number of possible searches was 30. Model parameters (table M2) were: $m = 20$; $k = 0.1$.

In general, mean occupancy increased with cluster size, percentage of suitable sites, and percentage of the landscape in clusters. Beyond clusters of about size 20, however, changes in landscape percentage had little effect on mean occupancy. This result was a consequence of our assumptions about the behavior of dispersing juveniles. With 20 suitable sites per cluster, a successful dispersal event usually occurred within the natal cluster. With fewer suitable sites, or smaller clusters, birds were forced to leave their natal cluster and entered the surrounding forest matrix. As a consequence, they experienced a lower likelihood of successful dispersal (equation 2).

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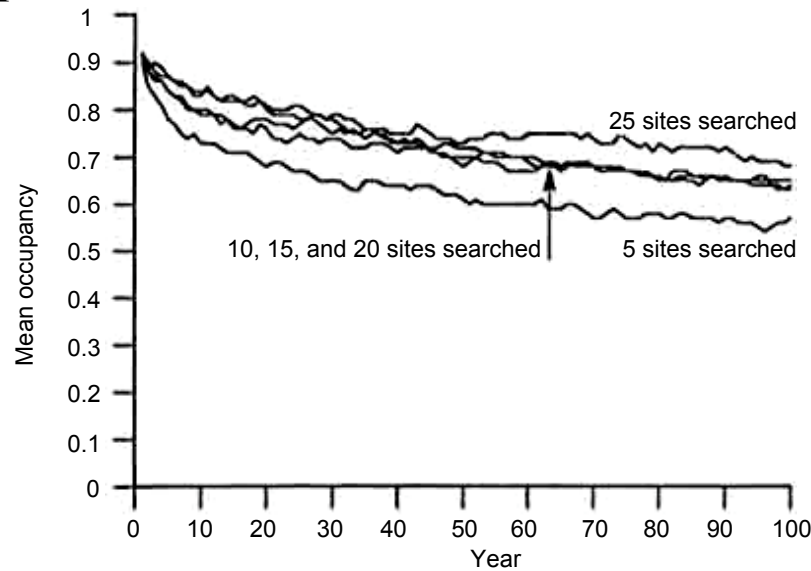


Figure M24—Mean cluster occupancy proportion against time for a 100-year simulation. The number of sites searched per cluster was varied from 5 to 25. Cluster size was fixed at 20; 50% were suitable. Model parameters (table M2) were: $h = 35\%$; $a = 20$; $p = 50\%$; $m = 12$; $k = 0.1$.

Varying Within-Cluster Search Efficiency

The cluster size at which mean occupancy stabilized was affected by the number of sites that were assumed to be searched within the natal cluster before dispersal into the surrounding landscape matrix (equation 1). To explore the sensitivity of mean occupancy to variation in search, we systematically varied the number of sites searched in the natal cluster (fig. M24). We assumed 20 sites per cluster, 100% suitable, and $k = 0.1$. Given clusters of this size, the mean occupancy was relatively insensitive to variation in within-cluster search efficiency. For example, the difference in equilibrium occupancy between 25 sites searched and 5 sites searched was 0.1 (0.68 - 0.58; fig. M24). When cluster size was decreased to <10 sites per cluster, however, the effect of low within-cluster search efficiency became significant, particularly when cluster populations were near their carrying capacity.

Varying Between-Cluster Dispersal

The sensitivity of model results to variation in the distance between clusters was most directly evaluated by estimating the sensitivity of mean occupancy to variation in the dispersal coefficient (equation 2). For this simulation, we assumed clusters of size 5 with all sites suitable. All other model parameters were as before, except that up to five clusters could be searched. With clusters of size 5, even with opportunity to search five clusters, varying the dispersal coefficient strongly affected mean occupancy (fig. M25). Given high resistance to dispersal within the matrix ($k = 1.0$), no equilibrium was reached, and the populations went to extinction. When the matrix offered little resistance to dispersal ($k = 0.03$), mean occupancy equilibrated at a high value. Other values of k showed intermediate results.

The significance of between-cluster dispersal strongly depended on cluster size. For example, a simulation based on 20 sites per cluster, with 50% of the sites suitable, was relatively insensitive to variation in k (fig. M26): all coefficients supported a long-term equilibrium in mean occupancy. The difference in the 100-year level of mean occupancy between $k = 0.03$ and $k = 0.30$ was about 0.12. Thus, to the extent that our between-cluster dispersal equation (2) reflects reality, we conclude that cluster size is more important than cluster spacing.

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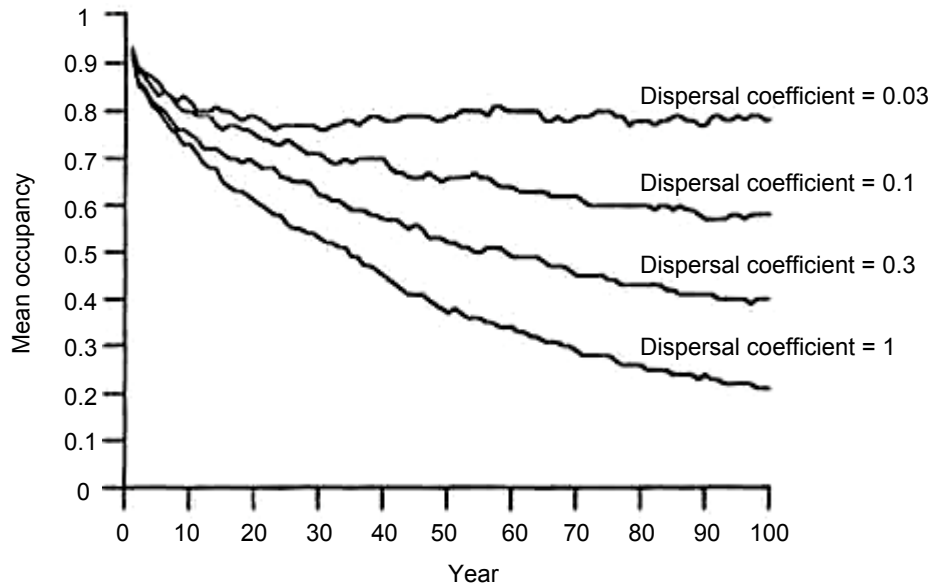


Figure M25—Mean cluster occupancy proportion against time for a 100-year simulation for four values of the dispersal coefficient. A maximum of five clusters could be searched. Model parameters (table M2) were: $h = 35\%$; $a = 5$; $p = 100\%$; $m = 12$; $k = 1.0$, 0.3, 0.1, 0.03.

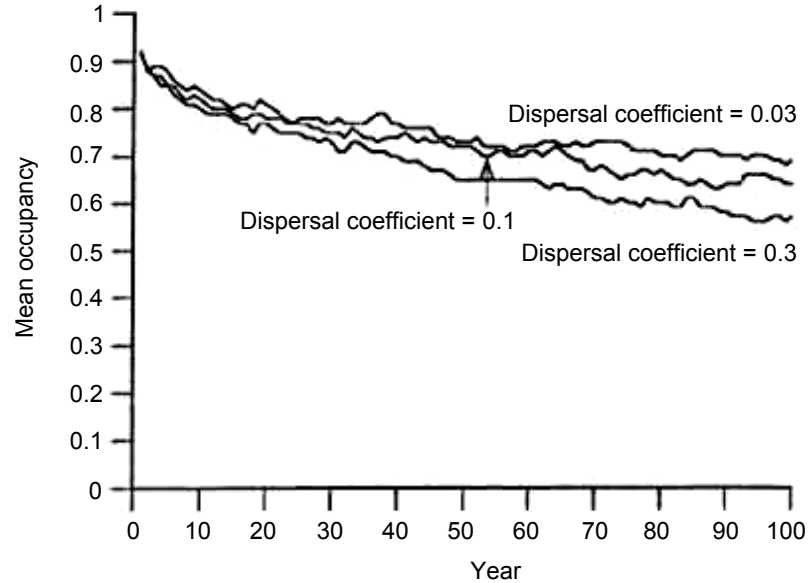


Figure M26—Mean cluster occupancy proportion against time for a 100-year simulation for three values of the dispersal coefficient. Cluster size was 20, 10 of which were suitable. Model parameters (table M2) were: $h = 35\%$; $a = 20$; $p = 50\%$; $m = 12$; $k = 0.3$, 0.1, 0.03.

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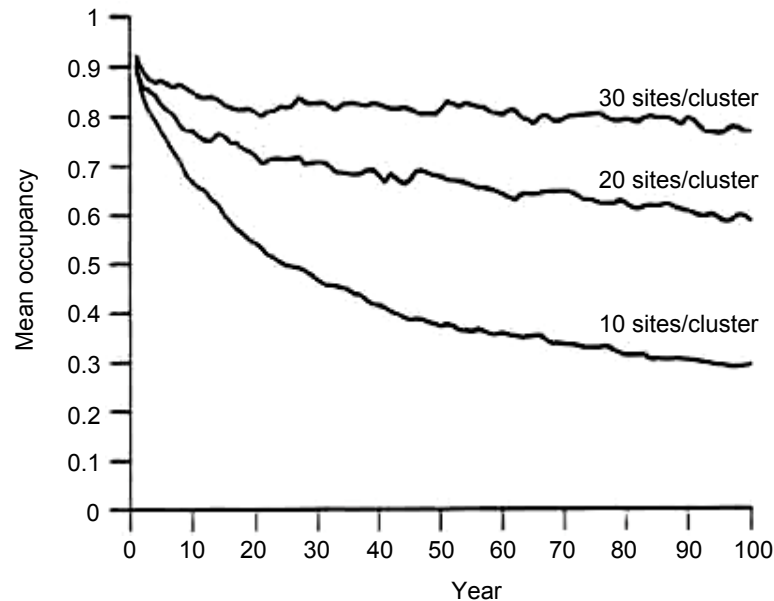


Figure M27—Mean cluster occupancy proportion against time for various numbers of sites per cluster. The total number of possible searches was 30. For 30 sites per cluster, 10 searches occurred within the natal cluster before emigration; for 20 sites per cluster, 6 searches; and for 10 sites per cluster, 3 searches. Model parameters (table M2) were: $h = 25\%$; $p = 60\%$; $k = 0.1$.

Allocating More Search-Time Outside the Natal Cluster

We assumed that juvenile owls systematically search within their natal cluster for a vacant territory before entering the forest matrix to search for another cluster. If dispersing juveniles move randomly rather than systematically, however, they will leave the natal cluster sooner and spend more time moving through the forest matrix. Thus, a consequence of our assumption about owl movement was an overestimation of mean occupancy. To investigate the magnitude of this effect, we performed several simulations, based on a fixed number of searches, that forced dispersing owls to expend much more of their search effort outside the natal cluster. The general result was a reduction in equilibrium mean occupancy (fig. M27); for clusters of size 20, for example, the reduction was 20%. Mean occupancy was reduced because more owls were moving through the forest matrix. This behavior reduced both the likelihood of finding a vacancy within the natal clusters and the number of potential colonists arriving at a cluster. Collectively, these behaviors substantially reduced equilibrium mean occupancy.

Effects of Initial Population Size

The effects of total population size strongly depend on the spatial arrangement of that population number. For example, our models suggested that, for a given population size, if the population was arranged in clusters of five, it would slowly go to extinction (fig. M15). In contrast, if that same population number was arranged in clusters of 20, the population had a much higher likelihood of persisting beyond 100 years (fig. M15). An additional question was the effect on mean occupancy of initializing the simulation at different population sizes for a fixed cluster size. We explored this relation by assuming 20 sites per cluster, 75% of the sites suitable, and 12 searches per cluster (fig. M28). An initially low population (for example, 40 pairs) increased, but only very slowly. Even after 100 years, this population had achieved $<1/2$ the occupancy of the population initialized with 360 pairs. The

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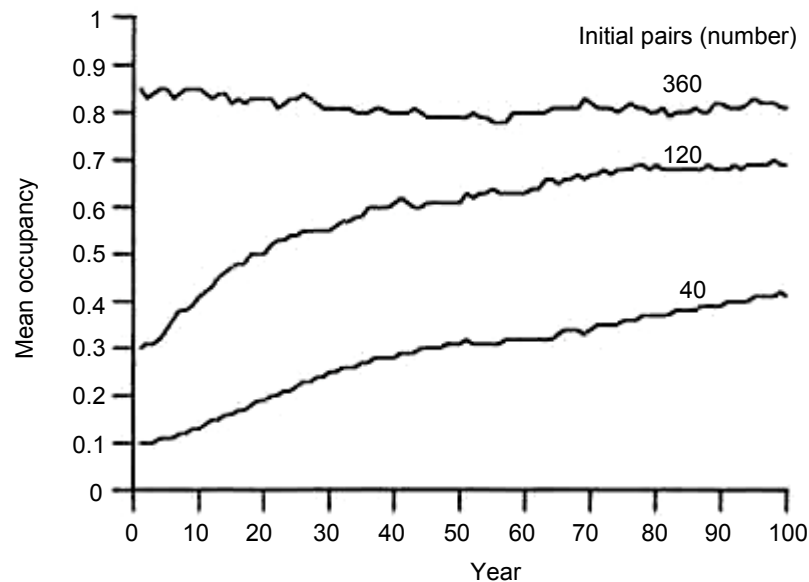


Figure M28—Mean cluster occupancy proportion against time for a 100-year simulation for three initial population values. Cluster size equaled 20, 75% of which were suitable. Model parameters (table M2) were: $h = 35\%$; $c = 20$; $p = 75\%$; $m = 12$; $k = 0.1$.

relation was nonlinear; however, because after 100 years, a population initialized with 120 pairs had attained about 80% of the occupancy of the population initialized with 360 pairs.

Discussion— Territory-Cluster Model

Our model results support some general conclusions that may prove useful in developing the spotted owl conservation plan. Similar to the findings of Doak (1989), our results suggest that providing for clusters of territories should increase the persistence likelihood of spotted owls, primarily by facilitating juvenile dispersal. Estimating a critical cluster size for a high likelihood of persistence is difficult, if not impossible, at this time. Within the structure of our model, clusters ≥ 15 sites appeared stable; if all sites were initially suitable, at least moderate connectivity existed among clusters, and dispersing owls searched preferentially within their natal cluster. Under more realistic conditions where many spotted owl HCAs would not be continuous habitat, either initially, or ever, stability seemed to require at least 20-pair clusters and low to moderate connectivity, individual spotted owls that are members of a large cluster population become less susceptible to the uncertainties of between-cluster dispersal and the character of the landscape matrix.

Cluster size, and the percentage of suitable sites, were highly interdependent. Suitable territories are less contiguous in HCAs that are below their potential carrying capacities. Successful within-HCA dispersal becomes more uncertain, rates of territorial replacement are lower when birds die, and more time is spent traveling through the surrounding forest matrix. Collectively, these factors all contribute to lower survival and fecundity rates and increase the risks to long-term viability.

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Further, our results suggest that a conservation network that provides only for individual pairs, or small clusters of pairs, has a low likelihood of providing for the continued existence of the species. In fact, even relatively large HCAs for spotted owls have uncertain fates, if they are currently far below their eventual carrying capacity. Such areas will need to be closely monitored until habitat within them has had time to recover. A way of increasing the certainty of their success is to initially position them close to large clusters (HCAs) that are nearer their potential carrying capacities.

Models of the population dynamics of long-lived vertebrates are difficult to validate. At this time, perhaps the best confirmation of our model inferences is that they are generally supported by the results from empirical studies (appendices N, O, P). The output and inferences drawn from a model, however, are always a reflection of the model's structure, and our model is no exception. Clearly, the patterns we observed in our simulations reflect the model's structure and the assumptions we made about spotted owl behavior. The usefulness of models can be defended to some extent if they accurately reflect key aspects of the species' ecology and behavior. We have attempted to structure our model in ways that reflect how we understand owls to behave. In some aspects of model structure, such as basic life-history patterns and the values of birth and death rates, we have more certainty than in others. For example, our model and its results are clearly the consequence of assumptions we have made about the dispersal behavior of juvenile owls within and between territory clusters. Unfortunately, little is known of spotted owl dispersal behavior and owl movement patterns through heterogeneous landscapes.

One inference drawn from our results—the positive effect of increasing cluster size—has much stronger support in both empirical and theoretical studies. Populations quickly escape from the dangers of demographic stochasticity with even slight increases in population size (Goodman 1987). Populations also gain security from environmental uncertainty with increasing numbers but at a much slower rate than from demographic effects (Shaffer 1987). Therefore, this model result was not surprising. Of interest, however, was the fact that marginal gains in mean occupancy were not constant with incremental increases in cluster size. Rather large gains resulted in moving from clusters of size 5 to clusters of size 10; much smaller gains were realized in moving from 10 to 20 territories per cluster.

In our individual-territory model, we assumed that all sites were equally likely to be searched until a suitable site was located or until the search capabilities were exceeded (that is, the owl died). The probabilities of finding a suitable site, or an individual of the opposite sex, became insurmountable when suitable habitat was less than about 20% of the landscape, or when the population was too low. The landscape was essentially infinite in scale but with distinct habitat boundaries (that is, we did not include edge effects).

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In our second model, we invoked the concept of clusters, groups of two or more adjacent suitable sites. If a single, very large cluster is created with reflecting boundaries; however, it can begin to act just like our first model. If we begin to decrease the percentage of this large block that is suitable habitat and set limits to search, we can demonstrate the same behavior as in the first model. Our cluster model did not have reflecting boundaries, but owls searched preferentially within their natal cluster before searching the matrix for another cluster. Because the total number of searches was finite, if the cluster was large enough the bird never searched outside the cluster. It simply exhausted its search capabilities before ever leaving its natal cluster. For very large blocks then, the model can behave as if the boundaries are reflecting and virtually no movement occurs outside of clusters. Large clusters become very stable, and the model becomes insensitive to dispersal, and thus distance, between clusters. If spotted owls do not show strong preference for searching within clusters, then the suitability of the surrounding matrix becomes considerably more important. Assuming a fixed search effort, if less preference is shown for within-cluster search, then more effort must be spent searching among clusters. An important consequence of expending more search effort in the matrix is that the necessary cluster (HCA) size to achieve a given occupancy is increased.

If dispersing owls do preferentially search their natal cluster before entering the matrix, some long-term genetic consequences are possible. The general effect of subdividing the owl population into HCAs may be to slightly increase the total genetic variation in the metapopulation, but at the expense of decreasing genetic variation within HCAs (see Lande and Barrowclough 1987). Very large HCAs produce high demographic stability, but may lead to a decline in genetic variation from inbreeding. Smaller HCAs promote higher dispersal rates but may lead to demographic instability. Therefore, some optimal size for an HCA probably exists that achieves a balance between these two processes.

The extent to which our model results reflect the key consequences of movement in a spatially heterogeneous landscape is unknown. We assumed that risks to owl viability were more pronounced from demographic than genetic factors. This could be a significant omission if, for example, we have overestimated the vagility of dispersing owls in the forest matrix. If this is true, then there may be possible deleterious genetic effects from inbreeding within the large HCAs. We developed a model that we believe to be compatible with what is currently known about owl life-history structure, dispersal behavior, and population dynamics. To have a higher degree of confidence in the generality of our model results, however, will require a considerably deeper understanding of how spotted owls move through their environment and respond to habitat heterogeneity at a variety of spatial scales.

References

- Allee, W. C. 1931. Animal aggregations. The University of Chicago Press, Chicago, Ill.
- Allee, W. C. 1938. The social life of animals. W.W. Norton and Company, New York.
- Boyce, M. S. 1987 unpubl. A review of the U.S. Forest Service's viability analysis for the spotted owl. Final report to the National Council of the Paper Industry for Air and Stream Improvement. 50pp.

Appendix M: Population Models

- Dennis, B. 1989.** Allee effects: Population growth, critical density, and the chance of extinction. *Nat. Resour. Modeling* 3:481-538.
- Doak, D. 1989.** Spotted owls and old growth logging in the Pacific Northwest. *Conserv. Biol.* 3:389-396.
- Franklin, A. B., J. A. Blakesley, and R. J. Gutiérrez. 1990 unpubl.** Population ecology of the northern spotted owl in northwestern California: Preliminary results, 1989. Final report submitted to the For. Serv. and the Calif. Dep. Fish and Game. 31 pp.
- Goodman, D. 1987.** The demography of chance extinction. Pp. 11-34 in M. E. Soule, ed. *Viable populations for conservation*. Cambridge Univ. Press, Cambridge, U.K. 189pp.
- Lamberson, R. H., R. McKelvey, B. R. Noon, and C. Voss. 1989 unpubl.** The effects of varying dispersal capabilities on the population dynamics of the northern spotted owl: preliminary results.
- Lande, R. Pers. comm.** Univ. of Chicago, Dep. Ecol. and Evolu., Chicago, Ill.
- Lande, R. 1987.** Extinction thresholds in demographic models of territorial populations. *Amer. Nat.* 130:624-635.
- Lande, R. 1988.** Demographic models of the northern spotted owl (*Strix occidentalis caurina*). *Oecologia* 75:601-607.
- Leslie, P. H. 1945.** On the use of matrices in certain population mathematics. *Biometrika* 33:183-212.
- Leslie, P. H. 1948.** Some further notes on the use of matrices in population mathematics. *Biometrika* 35:213-245.
- Lefkovich, L. P. 1965.** The study of population growth in organisms grouped by stages. *Biometrics* 21:1-18.
- Marcot, B. G., and R. Holthausen. 1987.** Analyzing population viability of the spotted owl in the Pacific Northwest. *Trans. N. Amer. Wildl. Nat. Resources Conf.* 52:333-347.
- Noon, B. R., and C. M. Biles. 1990.** The mathematical demography of the spotted owl in the Pacific northwest. *J. Wildl. Manage.* 54:18-27.
- Shaffer, M. 1987.** Minimum viable populations: coping with uncertainty. Pages 69-86 in *Viable populations for conservation*. M. F. Soulé, ed. Cambridge Univ. Press, Cambridge, U.K.

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U.S. Department of Agriculture, Forest Service. 1988. Final supplement to the environmental impact statement for an amendment to the Pacific northwest regional guide. Two volumes. U.S. Department of Agriculture, Forest Service: Portland, Oreg.

Extinction of Species and Populations

Causes of Extinction

Our goal is to develop a plan that will ensure long-term survival of the northern spotted owl in well-distributed numbers throughout its range. In developing such a plan, reviewing factors known to cause species to disappear from all or portions of their native ranges is instructive.

As noted by Shaffer (1981), factors leading to population extinction fall into two broad categories: systematic pressures and stochastic perturbations. Systematic pressures are such factors as habitat loss, toxic substance accumulation in the environment, or unrelenting resource harvesting by humans. The ivory-billed woodpecker, for example, vanished from the southeastern United States when virgin bottomland forests in which it nested and foraged were cleared (Tanner 1942). The peregrine falcon, osprey, and bald eagle all experienced major population declines after World War II as a result of the widespread use of DDT and other persistent pesticides (Halliday 1978). And the passenger pigeon and Carolina parakeet were exterminated in large measure by hunting (Blockstein and Tordoff 1985).

Stochastic perturbations that affect population persistence fall into four categories: genetic deterioration, demographic stochasticity, environmental stochasticity, and metapopulation dynamics.

Genetic Stochasticity

Genetic stochasticity involves changes in gene frequencies from such factors as inbreeding and founder effects. Loss of genetic variability in populations can lead to reduced fertility, the establishment of deleterious traits within a population, or the inability to adapt to sudden environmental changes (Allendorf and Leary 1986, Ledig 1986, Ralls et al. 1986). Inbreeding and population bottlenecks, which can lead to a loss of genetic variability, are serious problems for small, isolated populations. Because interpatch dispersal is facilitated by management of the landscape matrix surrounding the HCAs that we propose (appendix P), deleterious genetic phenomena associated with small population size should not affect the persistence of the spotted owl under this conservation strategy.

Demographic Stochasticity

Demographic stochasticity is defined as chance events in the reproduction or survival of a finite number of individuals. For species that reproduce sexually, a healthy population must have not only enough individuals, but also the right mixture of sexes and the right age-structure. A highly skewed sex ratio, periods of poor reproduction, or excessive mortality of a particular age-class can threaten the long-term survival of some populations. To cite an extreme example, when the last six dusky seaside sparrows all turned out to be males, the recovery of this endangered bird became impossible. Some species may require a threshold number of individuals to avoid social dysfunction and to breed successfully. Below this threshold, individuals do not reproduce successfully at rates high enough to sustain the population. This problem might be expected to be most acute for species that

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breed in colonies. The HCAs, which are designed to support substantial numbers of owl pairs, should serve to lessen the negative consequences that small population sizes have on demographic factors that bear on spotted owl persistence (see appendix O).

Environmental Stochasticity

Environmental stochasticity refers to temporal variation in habitat attributes, as well as populations of competitors, predators, parasites, and diseases. Under most circumstances, environmental variation does not pose a serious threat to a large, well-distributed population. But when that population is much reduced in size or distribution, these temporal changes can push it towards extinction. Ehrlich et al. (1980), for example, document the extinction of several small butterfly populations during a 2-year drought in central California.

Natural catastrophes include the most extreme environmental events that affect population persistence. Fires, storms, and disease epidemics are rare events in the lifetime of the individual organism, but over long enough periods of time, such events inevitably occur, and they can eliminate both habitats and the populations they support. For example, an epidemic of canine distemper reduced the only sizable population of the endangered black-footed ferret from 128 individuals to about 18 in less than a year (May 1986). The Mount St. Helens eruption destroyed thousands of acres of habitat suitable for the spotted owl, as did fires in the Klamath National Forest in 1987.

Environmental stochasticity and catastrophes have been considered in this conservation strategy. The many large HCAs, distributed across a three-State region, should reduce to essentially zero the chance that environmental events, even of considerable magnitude, will threaten the spotted owl throughout its range (see appendix O).

Metapopulation Effects

Most species persist regionally as metapopulations, sets of populations that are linked by dispersing individuals, allowing for the recolonization of unoccupied habitat patches after local extinction events. Loss of suitable habitat patches, or disturbances in the surrounding landscape matrix, can disrupt metapopulation dynamics and this loss can contribute to the regional extinction of a species. Metapopulation dynamics have been documented for a wide variety of species from invertebrates (Bengtsson 1989), to cold-blooded vertebrates (Sjorgen 1988), to mammals (Smith 1980). All exhibit discrete local populations that are subject to extinction but regionally persist through recolonization from surviving neighboring populations. The spacing of HCAs and the character of habitats in the interconnecting landscape matrix specified for this conservation strategy (see appendices P and O) will facilitate the exchange of individual owls among available habitat patches. This design feature should preclude the isolation of habitat patches and of the demographic units that they support; hence, it should contribute to the persistence of interacting demographic units.

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Effects of Stochastic Perturbations

Stochastic perturbations have two important aspects. First, the smaller and more isolated a population is, the more vulnerable it is to genetic, demographic, and environmental perturbations, and to metapopulation disruption. Natural catastrophes, of course, can be destructive to both large and small populations. Second, stochastic perturbations differentially operate at different population sizes. A population large enough to avoid inbreeding may still be vulnerable to extinction from demographic fluctuations (such as the presently isolated population of spotted owls on the Olympic Peninsula). For wild populations in natural environments, therefore, demography is likely to be of more immediate importance than genetics in determining population viability (Lande 1988). Finally, stochastic perturbations normally act in concert and, in so doing, may accelerate the demise of a population. The best example of this acceleration is probably the heath hen (see Shaffer 1981, Dawson et al. 1986).

Originally abundant from New England to Virginia, the heath hen steadily declined as European settlement advanced. By 1876, heath hens survived only on Martha's Vineyard Island, Massachusetts. A refuge was established for the birds, and efforts were made to eliminate their predators. By 1915, heath hens could be found all over the island, and the population was estimated at 2000. In 1916, a fire destroyed most of the nests and habitat, and the following winter brought an invasion of predatory goshawks from the north. These two catastrophic events reduced the population to 100 to 150 individuals. The birds gradually increased, to about 200 in 1920. That year, an epidemic disease reduced the population to less than 100 individuals. The remaining birds appeared to become increasingly sterile (perhaps because of genetic deterioration), and the population as a whole suffered from an excess of males (contributing to demographic imbalance). The last heath hen disappeared in 1932.

Important lessons can be learned from this example. A once widespread and abundant species was driven to extinction by habitat destruction and hunting pressure, which reduced its range to a small island and its numbers to a few hundred individuals. At that size, it was vulnerable to several stochastic perturbations. Had other populations been spared, heath hens might have survived the unfortunate but inevitable sequence of catastrophic events in their island refuge.

Similar phenomena currently place the spotted owl at risk. Systematic timber harvesting and, to a much lesser degree, stochastic natural environmental phenomena act in concert to destroy and fragment superior and suitable habitat for the owl.

We know that habitat loss, in particular, can facilitate extinction by turning large populations into smaller, more isolated ones. It does so through the process of habitat fragmentation, which occurs wherever a large, contiguous habitat is transformed into smaller patches that are isolated from each other by a landscape matrix unlike the original (Wilcove et al. 1986). This matrix can differ from the original habitat in either composition or structure; the crucial point is that it functions as either a partial or total barrier to dispersal for species associated with the original habitat. We must be careful to distinguish between fragmentation that isolates pairs and populations, and fragmentation within the home range of individual pairs. The former type of fragmentation is a clear threat to population viability. Owls on the Olympic Peninsula, for example, are demographically isolated as a result of habitat loss. The extent to which fragmentation within a home range

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is harmful is less well known. Individual owls tend to increase their home-range size in response to fragmentation (Carey et al. 1990, Forsman et al. 1984). The increase in home range may increase the risk of predation or place increased energetic demands on the birds as they forage. Data are insufficient to confirm or refute these hypotheses. Spotted owls can sustain some amount of fragmentation within their home ranges, however, as demonstrated by the presence of breeding owls in fragmented BLM lands in western Oregon.

The habitat conservation strategy proposed in this document describes specific habitat features for the landscape matrix surrounding HCAs. Those features (including retention of 50% of the forest in that landscape matrix in trees at least 11 inches in d.b.h., totaling at least 40% canopy cover—see appendices P and O) significantly reduce the contrast between HCAs and the surrounding landscape in which they are embedded. Combined with the large size of HCAs, the conservation strategy should adequately mitigate many of the negative consequences of habitat fragmentation as it affects populations.

Other Factors

In addition to these systematic and stochastic factors that cause extinctions, four mechanisms involving habitat fragmentation lead to extinction: edge effects and the influx of species from the outside matrix, secondary extinctions among coevolved species, loss of critical microhabitats, and loss of habitat refugia.

Edge Effects

Discontinuities between ecological communities are among the most striking features of natural landscapes. Dramatic edges between habitat types not only contribute texture and physical diversity to ecosystems, they are primary determinants of regional species diversity. Wildlife biologists have long recognized that different habitat types support different sets of species and that the edges between habitats can be particularly rich in game species. Indeed edges between habitats often serve as distinct habitats themselves, supporting unique suites of edge-dependent species.

Those concerned with the conservation of certain forest-dwelling species, however, have noted that the increased ratios of forest edge to forest interior, which inevitably result from forest fragmentation, can have strong negative impacts on those species (Temple and Cary 1988, Whitaker 1980, Whitcomb et al. 1976, Wilcove 1985, Wilcove et al. 1986, Yahner 1988). Invasion by edge-dwelling species into interior environments can be a major threat to the survival of forest interior species (Ranney et al. 1981). For example, in the Eastern United States, edge-dwelling species include numerous predators and brood parasites of forest interior songbirds (Brittingham and Temple 1983, Whitcomb et al. 1981). As Harris (1988) points out, the magnitude of such “edge effects” tends to be inversely proportional to the quality of adjacent habitat patches; hence, the more extreme the structural difference across habitat edges, the more dramatic the effects on interior species.

Several scientists have hypothesized that predation on spotted owls by great horned owls, and competition from barred owls, may increase with increasing amounts of forest edge associated with the harvest of mature and old-growth timber. The abrupt edges created by clearcutting are also likely to increase the amount of blow-down in mature and old-growth timber, thereby reducing the amount of suitable spotted owl habitat. The extent to which this poses a serious problem in the conservation of the northern spotted owl is unknown (also see appendix O).

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Secondary Effects and Extinctions

The scientific literature is replete with examples of interconnected life. Indeed the term “coevolution” was coined specifically to describe the evolution of mutualistic relationships or other interdependencies among species. Examples abound that document how the decline or loss of one species can produce a cascade of secondary effects that can range from the disruption of ecosystem functions, to an alteration of the population dynamics of surviving species, and even to additional extinctions (Gilbert 1980, Terborgh and Winter 1980, Wilcove et al. 1986).

For most ecosystems, the potential impact of a single species lost is impossible to determine a priori. For comparatively simple ecosystems with relatively low diversity, however, the role of a “keystone” species in ecosystem function may be relatively straightforward, and the effects of its removal may even be determined experimentally (Paine 1966). Large vertebrates certainly appear to play dominant roles in a wide variety of ecological communities, and their loss can have profound and immediately measurable effects.

A notable example can be drawn from studies on Barro Colorado Island, a former hilltop that became an island when the Chagres River was dammed during construction of the Panama Canal in 1914. Large predators such as jaguars, pumas, and harpy eagles quickly disappeared from the island. Perhaps because their main predators were gone, a variety of medium-sized mammals are now remarkably abundant. These include the collared peccary, agouti, coatimundi, and armadillos (Terborgh and Winter 1980). Many of these mammals are voracious consumers of bird eggs and young. Their abundance is thought to be one reason why 15 to 18 species of forest-dwelling birds have vanished from Barro Colorado island (Willis 1974; but see Karr 1982 for evidence that the number may be considerably larger than that). Many of these birds share the trait of nesting on or near the ground.

Some of the best examples of how loss of a certain species can lead to secondary extinction are found in complex tropical ecosystems (for example, see Gilbert 1980, Terborgh 1974), although temperate-zone examples involving plants and invertebrates (Thomas 1976), small mammals and birds (Matthiae and Stearns 1981, Whitcomb et al. 1981), and dominant herbivores and predators (Wilcove et al. 1986) are common. Soulé et al. (1988) present evidence that the loss of coyotes from small, isolated patches (“islands”) of chaparral habitat in California leads to secondary losses of native birds, in part attributable to increases in the numbers of small predators that were once kept in check by the coyotes.

The disruption of ecosystems, or the loss of additional species, is most likely to occur where a large, long-lived species that dominates a specific ecosystem function is at risk (Terborgh 1988). The role of the northern spotted owl as a predator of numerous small mammal species makes it an apt example of one such predatory species, the loss of which might well compromise ecosystem integrity and affect the population dynamics or persistence of co-occurring species.

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Microhabitats

Certain large-scale habitat landscape features are so clearly key to the survival of a species that loss of those features would assure the species' demise. The availability of prairie grassland for bison and shifting dune sand for fringe-toed lizards are obvious examples. Often, however, local species survival depends on the availability of specific microhabitats: small portions of a habitat providing resources or environmental conditions critical to some phase of the organism's life history. Conservation planning can be particularly challenging when microhabitats prove to be important to population persistence. Indeed, reserves based only on broad habitat requirements may very well fail if subtle or cryptic microhabitat requirements are overlooked.

The threatened bay checkerspot butterfly serves as a good illustration of how microhabitat suitability can vary across landscapes and through time (Murphy and Weiss 1988, Weiss et al. 1988). Although the host plants of the butterfly are distributed widely across its grassland habitats, the development and survival of its larvae vary greatly between slope exposures, and from one year to another. Populations in habitats without cool exposures are highly susceptible to local extinction from drought. Habitats without warm exposures may delay adult flight periods too late for reproduction to occur in some years. A full range of topographically defined microhabitats in a habitat patch helps to ensure that at least some individuals are in phase with host plant resources in all growing seasons. Furthermore, a proximate spatial arrangement of cool and warm microhabitats can facilitate dispersal between them, thus allowing larvae to respond to short-term variation in habitat quality.

Population dynamics of large, long-lived species may not respond as dramatically to fine-scale variation in habitat condition as do the butterflies. Spotted owls, however, do respond to the microclimates within their territories, choosing cooler or warmer spots in response to seasonal or even daily fluctuations. Thermoregulation has been cited as one reason why the owls are closely associated with structurally complex, mature and old-growth forests. Moreover, some of the small mammal prey species on which the spotted owl largely depends seem to depend on the availability of certain microhabitats: for example, those associated with microclimatic conditions (Belk et al. 1988, Getz 1965, Hoffman 1984) and specific resources (for example, fungi for flying squirrels, Maser et al. 1981) that may be narrowly distributed.

Habitat Refugia

Both empirical evidence and common sense suggest that not all available habitat is equal, either in quality or importance to the persistence of populations. Certain portions of habitat may provide sparse resources, or resources may be available only during certain periods. Such habitat might be viewed as marginal in value to population persistence (appendix F). By contrast, other habitat may provide a full range of resources that are constantly available through time. Such habitat not only may be suitable, but it may also provide a refuge for individuals during environmental extremes that may render less-suitable habitat unavailable. Conservation planning that does not consider the differential ability of specific habitat areas to support target species at minimum population sizes through time may fail—even where extensive suitable habitat is protected, managed, or both. Habitat refugia are particularly important to the persistence of species in regions where environmental extremes are commonplace.

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How habitat refugia can determine long-term persistence of animal populations is well illustrated by the Amargosa vole, a resident of a highly circumscribed marsh habitat in the Mojave Desert. Low-elevation habitat (that within the floodplain of the Amargosa River) constitutes nearly 90% of the area supporting resources for the vole. But that habitat is annually flooded and rendered uninhabitable. Habitat at moderate elevation floods less often (on the order of every 30 years or so) and is inhabitable between such events. At such times, the small percentage of habitat at the very highest elevations provides the only refuge for the species; hence, a small fraction of total habitat is absolutely essential to the persistence of the vole. Reserve design must include that habitat to achieve conservation of the species.

The recurrence of major natural catastrophes this century that have impacted significant portions of the distribution of the northern spotted owl (for example, the “blow-down” of 1921 on the Olympic Peninsula and the wildfires of 1987 in the Klamath Region), demonstrates that conservation planning for the owl must consider habitat refugia. Furthermore, during intensive harvest of private timberlands in the early 1900s, the owl was sustained by habitat on FS lands that then provided refugia. The conservation strategy should assure habitat refugia, especially in larger HCAs, and many of these should be at lower elevations at inland locations.

Additional Factors

Three additional factors associated with habitat fragmentation must be considered in developing an effective conservation plan for the northern spotted owl: thresholds, packing phenomena, and the role of unoccupied habitat in the long-term survival of a population or species.

Thresholds

Threshold phenomena occur when relatively small changes in some component of an ecosystem induce dramatic, large-scale changes in some other component or components. For example, “Below a certain level of pollution, trees will survive in smog, but when a small increment in the local human population produces a small increment in smog, living trees become dead. Perhaps 500 people can live around a certain lake and dump their raw sewage into it, and its natural systems will be able to break down the sewage and keep the lake from undergoing rapid ecological change. But 505 people may overload the system and result in a polluted or eutrophic lake” (Ehrlich et al. 1970:727).

We need to be mindful of the possibility of threshold phenomena for spotted owls (see appendix M). One reasonable possibility, for example, is the fragmentation of suitable habitat. As total suitable habitat area declines and the mean distance between patches of suitable habitat increases, spotted owls may be able to survive and reproduce at apparently safe rates up to some threshold, either in total area of suitable habitat, mean distance between patches, or both. But a small, added increment of habitat loss might then put the birds on a steep and irretrievable trajectory to extinction.

We know that any number of factors associated with fragmentation can push a population towards extinction. But often we cannot assess the absolute importance of any single factor. Nonetheless, if they act in concert or if important thresholds exist, a relatively small increase in any one could be sufficient to tip the scales toward extinction.

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Packing Phenomena

Because birds and mammals are relatively long-lived and mobile, they can temporarily escape from a place where their habitat is being degraded or destroyed and move into nearby patches of undisturbed habitat. Thus, for short periods, densities of individuals within undisturbed patches may increase, a phenomenon known as packing.

Lovejoy et al. (1986), for example, netted and banded birds in an area of Brazil where the primary forests were being cleared for cattle pasture. They discovered that capture rates of various species in a particular forest plot increased dramatically as nearby areas were cleared. Densities remained high for several months, but eventually dropped. They concluded that the increase represented an influx of displaced birds from areas that had been recently cleared. Given the territorial nature of many bird species and the fact that only a finite amount of food or cover is available in a given area, that the displaced birds were unable to persist indefinitely in the forest plot is not surprising.

A consequence of packing, therefore, is an anomalous increase in density in remaining local patches of suitable habitat by a species whose population may be otherwise in decline as a result of habitat loss. Such local increases in density are not necessarily indicators of “healthy” population status or adequate reproductive output. As discussed in appendix L, packing appears to be occurring in several locations within the current range of the spotted owl (for example, on BLM lands in southern Oregon, and the Willow Creek study area and the Mad River redwood area, both in Humboldt County, California). The phenomenon of packing underscores the need to assess population trends on as large a geographic scale as possible.

Unoccupied Habitat

The problem of identifying important habitat is magnified when that habitat is not permanently occupied by the species of concern. Migratory birds and salmon, for example, abandon some habitats for long periods; nonetheless, these areas are obviously essential to the survival of the species. More difficult to understand, however, is the role of unoccupied habitat for the many species that are neither migratory nor cyclical in their use of habitats. Is the unoccupied habitat of importance to their long-term conservation? The answer, in some cases, is yes. For these species, protecting unoccupied habitat can be as important to regional persistence as protecting of occupied habitat.

For species fitting this description, unoccupied habitat presents itself in two forms: as vacant habitat of marginal quality, contiguous with or adjacent to occupied habitat; and as distinct, separate, empty patches of high- or low-quality habitat. Unoccupied patches of either marginal or high-quality habitat can serve as occasional stepping stones for regional populations. These patches can facilitate gene flow between small populations and can provide routes for individuals to colonize surrounding habitats in which the species once occurred but is now gone. The loss of “stepping stone” habitat patches can even disrupt the dynamics of entire regional populations. For example, the once widespread and abundant Karner blue butterfly of the “pine bush” regions of New York and surrounding States disappeared from many regions as a result of the fragmentation and isolation of occupied and unoccupied habitat patches and the elimination of dispersal corridors.

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Habitat of marginal quality, such as locations with few food sources or nest sites, may support a given species only under certain circumstances. For example, marginal habitats that are normally empty may serve as the only refugia for plants and animals during times of fire, drought, or other environmental extremes. Under favorable conditions, marginal habitat may also boost the carrying capacity of an area. The resulting population expansion can buffer the population against future periods of environmental stress. Populations of the bay checkerspot butterfly are a classic example (Murphy and Weiss 1988, Weiss et al. 1988). Checkerspot populations live mostly on mesic, north-facing, grassland slopes. Years of above-average rainfall, however, allow the butterfly to expand its range into more xeric, south-facing slopes. Although infrequent and short-term, such expansions can contribute to long-term population persistence, especially for species whose numbers are usually regulated by environmental factors rather than by competition with other members of the same species.

Conclusions

The Committee has concluded that persistence of the spotted owl is presently at risk in significant portions of its range as a result of continued destruction, and concomitant fragmentation, of its habitat. This loss has included much of the habitat that appears to be superior for the owl, especially that at lower elevations. The result of this process has been the fractioning of a formerly more continuous population of spotted owls into smaller, isolated demographic units, many of which are at risk of local extinction because of demographic factors and environmental phenomena.

Local habitat fragmentation presents additional specific risks, including the possible deleterious effects of increased habitat edges and the attendant increased risk of predation on adults and young, the loss of crucial microhabitats that serve to lessen the effects of weather and provide for prey species, and the potential loss of key habitat necessary to provide refugia during catastrophic environmental occurrences.

The effects of habitat fragmentation on the persistence of the northern spotted owl may be partially reduced by conservation planning. A habitat conservation strategy that attempts to provide the owl with habitat distributed across the landscape in a fashion most similar to its historical configuration should provide the best hedge against future extinction. Studies of other species suggest that a plan that incorporates three key considerations will have a substantial likelihood of success. These considerations include providing multiple, extensive, and continuous areas of superior and suitable habitat; distributing these areas across the landscape at distances that encourage demographic interaction among them; and providing adequate connectivity in the form of surrounding landscape features to facilitate that demographic interaction (see appendix O and P).

References

- Allendorf, F., and R. Leery. 1986. Heterozygosity and fitness in natural populations of animals. Pages 57-76 in M. Soulé, ed. *Conservation biology: The science of scarcity and diversity*. Sinauer Associates, Sunderland, Mass.
- Beik, M. C., H. D. Smith, and J. Lawson. 1988. Use and partitioning of montane habitat by small mammals. *J. Mammol.* 69:688-696.
- Bengtsson, J. 1989. Interspecific competition increases local extinction rate as determined by a stand transect technique. *Ecol. Monogr.* 38:269-308.

Appendix N: Extinction

- Blockstein, D., and H. Tordoff. 1985.** Gone forever—a contemporary look at the extinction of the passenger pigeon. *Am. Birds* 39:845-851.
- Brittingham, M. C., and S. A. Temple. 1983.** Have cowbirds caused forest songbirds to decline? *BioScience* 33:31-35.
- Carey, A. B., J. A. Reid, and S. P. Horton. 1990.** Spotted owl home range and habitat use in southern Oregon Coast Ranges. 3. *Wildl. Manage.* 54:11-17.
- Dawson, W. R., 3. L. Ligon, J. R. Murphy, J. P. Myers, D. Simberloff, and 3. Verner. 1986.** Report of the advisory panel on the spotted owl. *Audubon Conserv. Rep.* 7. 47pp.
- Ehrlich, P. R., A. H. Ehrlich, and J. P. Holdren. 1970.** *Ecoscience: Population resources, and environment.* W. W. Freeman, San Francisco. 1052pp.
- Ehrlich, P. R, D. D. Murphy, M. C. Singer, C. Sherwoud, R. R. White, and I. L. Brown. 1980.** Extinction, reduction, stability, and increase: The responses of checkerspot butterfly populations to the California drought. *Oecologia* 46:101-105.
- Foreman, E. D., E. C. Meslow, and H. M. Wight. 1984.** Distribution and biology of the spotted owl in Oregon. *Wildl. Monogr.* 87:1-64.
- Getz, L. L. 1965.** Humidities in vole runways. *Ecology* 46:548-550.
- Gilbert, L. E. 1980.** Food web organization and conservation of neotropical diversity. Pages 11-34 *in* M. Soulé and B. Wilcox, eds. *Conservation biology: An evolutionary-ecological approach.* Sinauer Associates, Sunderland, Mass.
- Halliday, T. 1978.** *Vanishing birds: Their natural history and conservations.* Holt, Reinhart, and Winston. New York. 296pp.
- Harris, L. D. 1988.** Edge effects and conservation of biotic diversity. *Conserv. Biol.* 2:330-332.
- Hoffman, R. S. 1984.** Small mammals in winter: The effects of altitude, latitude, and geographic history. Pages 9-23 *in* J. F. Merrit, ed. *Winter ecology of small mammals.* Spec. Publ. Carnegie Mus. Nat. Hist. 10.
- Karr, J. R. 1982.** Avian extinction on Barro Colorado island, Panama: A reassessment. *Am. Nat.* 119:220-239.
- Lande, R. 1988.** Genetics and demography on biological conservation. *Science* 241:1455-1460.
- Ledig F. 1986.** Heterozygosity, heterosis, and fitness in outbreeding plants, Pages 77-104 *in* M. Soulé, ed. *Conservation biology: The science of scarcity and diversity.* Sinauer Associates, Sunderland, Mass.

Appendix N: Extinction

- Lovejoy, T. E., R. O. Bierregaard, Jr., A. B. Rylands, J. R. Malcolm, C. E. Quintela, L. H. Harper, K. S. Brown, Jr., A. H. Powell, G. V. N. Powell, H. O. R. Schubart, and M. B. Hays. 1986. Edge and other effects of isolation on Amazon Forest fragments. Pages 257-285 in M. Soulé, ed. Conservation biology: The science of scarcity and diversity. Sinauer Associates, Sunderland, Mass.
- Maser, C., B. R. Mate, J. F. Franklin, and C. T. Dyrness. 1981. Natural history of Oregon coast mammals. U.S. For. Serv., Gen. Tech. Rep. PNW-133. Portland, Oreg. 496pp.
- Matthiae, P. E., and F. Stearns. 1981. Mammals in forest islands in southeastern Wisconsin. Pages 55-66 in R. L. Burgess and D. M. Sharpe, eds. Forest island dynamics in man-dominated landscape. Springer Verlag, New York.
- May, R. 1986. The cautionary tale of the black-footed ferret. *Nature* 320:13-14.
- Murphy, D. D., and S. B. Weiss. 1988. Ecological studies and the conservation of the bay checkerspot butterfly, *Euphydryas editha bayensis*. *Conserv. Biol.* 46:183-200.
- Paine, R. T. 1966. Food web complexity and species diversity. *Am. Nat.* 100:65-75.
- Ralls, K., P. Harvey, and A. Lyles. 1986. Inbreeding in natural populations of birds and mammals. Pages 35-56 in M. Soulé, ed. Conservation biology: The science of scarcity and diversity. Sinauer Associates, Sunderland, Mass.
- Ranney, J. W., M. C. Bruner, and J. B. Levenson. 1981. The importance of edge in the structure and dynamics of forest islands. Pages 67-95 in B. L. Burgess and D. M. Sharpe, eds. Forest island dynamics in man-dominated landscapes. Springer Verlag, New York.
- Shaffer, M. L. 1981. Minimum population sizes for species conservation. *BioScience* 31:131-134.
- Sjorgen, P. 1988. Metapopulation biology of *Rana lessonae* on the northern periphery of its range. Ph.D. Dissertation. Uppsala University, Sweden.
- Smith, A. T. 1980. Temporal changes in insular populations of the pika (*Ochotona princeps*). *Ecology* 61:8-13.
- Soulé, M. E., D. T. Bolger, A. C. Alberts, J. Wright, M. Sorice, and S. Hill. 1988. Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. *Conserv. Biol.* 2:75-92.
- Tanner, J. T. 1942. The ivory-billed woodpecker. *Natl. Audubon Soc. Res. Rep.* 1. 111pp.
- Temple, S. A., and J. R. Cary. 1988. Modelling dynamics of habitat-interior bird populations in fragmented landscapes. *Conserv. Biol.* 2:340-347.

Appendix N: Extinction

- Terborgh, J. 1974.** Preservation of natural diversity: the problem of extinction prone species. *BioScience* 24:715-722.
- Terborgh, J. 1988.** The big things that run the world—a sequel to E. O. Wilson. *Conserv. Biol.* 2:402-403.
- Terborgh, J., and B. Winter. 1980.** Some causes of extinction. Pages 119-133 in M. Soulé and B. A. Wilcox, eds. *Conservation biology: An ecological-evolutionary approach*. Sinauer Associates, Sunderland, Mass.
- Thomas, J. A. 1976.** The ecology of the large blue butterfly, *Ann. Rep., Inst. for Terrest. Ecol.* 11:25-27.
- Weiss, S. B., D. D. Murphy, and R. R. White. 1988.** Sun, slope, and butterflies: topographic determinants of habitat quality for *Euphydryas editha*. *Ecology* 69:1486-1496.
- Whitaker, J. O., Jr. 1980.** The Audubon Society field guide to North American mammals. Chanticleer Press, New York.
- Whitcomb, R. F., J. F. Lynch, P. A. Opler, and C. S. Robbins. 1976.** Island biogeography and conservation: Strategies and limitations. *Science* 193:1030-1032.
- Whitcomb, R. F., C. S. Robbins, J. F. Lynch, B. L. Whitcomb, M. K. Klimkiewicz, and B. Bystrak. 1981.** Effects of forest fragmentation on avifauna of the eastern deciduous forest. Pages 125-205 in B. L. Burgess and D. M. Sharpe, eds. *Forest island dynamics in man-dominated landscapes*. Springer Verlag, New York.
- Wilcove, D. S. 1985.** Nest predation in forest tracts and the decline of migratory songbirds. *Ecology* 66:1211-1214.
- Wilcove, D. S., C. H. McLellan, and A. P. Dobson. 1986.** Habitat fragmentation in the temperate zone. Pages 237-256 in M. Soulé, ed. *Conservation biology: The science of scarcity and diversity*. Sinauer Associates, Sunderland, Mass.
- Willis, E. D. 1974.** Populations and local extinctions of birds on Barro Colorado Island, Panama. *Ecol. Monogr.* 44:153-169.
- Yahner, R. H. 1988.** Changes in wildlife communities near edges. *Conserv. Biol.* 2:333-339.

A Rationale for the Size and Spacing of Habitat Conservation Areas for Spotted Owls

Introduction

The literature of conservation biology describes many examples where the fragmentation of formerly widespread, terrestrial habitats into remnants of various sizes and degrees of isolation has resulted in the extinction of bird species from blocks of remaining habitat. Examples include alpine habitats in the northern Andes (Vuilleumier 1970), Barro Colorado Island in the Panama Canal Zone (Karr 1982, Willis 1974), New Zealand forests (Diamond 1984a, Williams 1981), Brazilian forests (Lovejoy et al. 1984, Willis 1980), the eastern deciduous forests of the United States (Forman et al. 1976, Whitcomb et al. 1981), Java woodlands (Diamond et al. 1987), and chaparral habitats in San Diego County, California (Soulé et al. 1988). The last example is especially interesting because it involved urban spread throughout once extensive stands of native chaparral vegetation.

Residential and other urban landscaping would seem to provide convenient and reasonably safe avenues of dispersal for chaparral-dependent birds to move between remnant patches of chaparral. As the work by Soulé and his colleagues shows, however, the distance between isolated patches of chaparral does not help to explain variation in the number of nonmigrant, chaparral-dependent species. Patch area (therefore, size of the original populations isolated) and the age since isolation explain most of the variation in numbers of chaparral-dependent species remaining in the patches. The vulnerability of a given species to local extinction was primarily explained by its original abundance in a patch and by its body size. Small populations disappeared at a high rate, and large-bodied birds were less extinction prone than small-bodied birds (as in the study by Pimm et al. 1988, described below). Soulé et al. conclude that virtually all chaparral-dependent species that exhibit little tendency to cross other habitat types are on an inevitable trajectory to extinction in the isolated patches of chaparral studied.

Recent focus on the role of habitat blocks in conservation biology has sparked much debate, discussion, and speculation. No specialist in the field, however, would dispute that habitat blocks should be a key component of a conservation strategy to assure the long-term persistence of a given species that is subject to widespread, systematic reduction in the amount of its suitable habitat. Much of the debate has focused on the "SLOSS" issue—whether a "single large or several small" blocks totaling the same area would be better for a reserve design (Diamond 1976, Simberloff and Abele 1976a, 1976b, 1982; Terborgh 1976, Whitcomb et al. 1976; see Shaffer and Samson 1985 for a recent summary). To the extent that the issue has focused on maintaining some amount of species richness in a region, we believe it has little relevance to the matter at hand. Our objective is to design a conservation strategy that assures the persistence of a single species—the spotted owl.

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Although certain lessons can be learned from evidence marshalled for this debate, our challenge is not one of enhancing species richness in Pacific Northwest forests. Our challenge is to design an arrangement of habitat conservation areas (HCAs) specifically for spotted owls, accounting for their densities, reproductive biology, dispersal capabilities, and so on.

Those aspects of the SLOSS debate, and of island biogeographic theory in general, that bear on the spotted owl issue deal with the likelihood of local extinction in relation to the sizes of habitat islands (thus potential population sizes) and the distances separating islands. Diamond (1975) proposed several design criteria from island biogeographic theory that are relevant here. Although Diamond's concepts stemmed from an objective of maintaining or increasing species richness, the fundamental principles seek to minimize the risk of extinction for all sorts of species. Thus, the same general principles apply to all species but "different species require different minimum areas to have a reasonable chance of survival" (Diamond 1975:129). The fundamental difference between examples from true oceanic islands, and "islands" of different types of habitat in an extensive landscape, has to do with dispersal events. Transoceanic dispersal by land birds is more risky than dispersal across a landscape where opportunities exist to stop, rest, and forage (see Wiens 1989 for further discussion of this point).

Designing a Conservation Strategy

The challenge for anyone designing a conservation strategy for a single species is to reconcile an ideal strategy with the real world. For spotted owls in the Western United States, habitat exists in a hodge-podge of gaps, troughs, and peaks in both distribution and abundance created by geographic, edaphic, topographic, climatic, and human-induced variety on the landscape. Once standards and guidelines have been devised for the ideal size and spatial arrangement of HCAs, we must then fit them as best we can to those real-world constraints.

The final size of a population provided by a conservation strategy is important, but it is not the only consideration. For example, most of Hawaii's endangered bird species now occupy less than 10% of their former range, even though a few have total populations estimated between 1000 and 10,000. But most of the nonendangered forest birds in Hawaii occupy more than 10% of their former range, and some of those populations are estimated between 100 and 1000 birds (Scott et al. 1988). We believe that a population of 3000 spotted owl pairs with one type of habitat distribution and structure could easily be less viable than a population of 1500 pairs in a habitat with different distribution and structure. Studies of efforts to reintroduce species into native areas from which they have been extirpated indicate that several factors affect the likely persistence of release populations (Griffith et al. 1989). Among these factors, the number of animals released (population size), and habitat quality in the release site, are points to consider in developing a conservation strategy for spotted owls.

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Once the strategy provides habitat for some number of pairs with a reasonably high chance of long-term persistence, other elements of the strategy may become more important than increasing total population size. These elements include the extent of geographic distribution, the spacing of breeding units, and the provision of sufficient habitat (see appendix F) to assure successful breeding. A successful strategy also requires assuring that dispersing juveniles have a high probability of locating and filling vacancies created by deceased territory holders, assuring that local distributions foster successful population dynamics, and assuring that social interactions vital to a population's success can take place. The point is that, once these elements are assured, populations in a wide range of sizes can have an excellent chance of persisting well into the future.

General Guidelines

Diamond offers some general guidelines for a conservation strategy. In general, we concur with them and believe they are consistent with recommendations by Harris (1984) and Noss and Harris (1986). We have outlined these guidelines below, with additional guidelines suggested from the work of den Boer (1981) and Wilcove et al. (1986). We believe the first five guidelines are equally and vitally important to a conservation strategy for spotted owls. But we have been mindful, as well, of the messages imparted by the remaining three.

- We begin by adding to Diamond's list den Boer's (1981) notion of spreading the risk. Ideally, blocks of habitat should be dispersed in a pattern corresponding to a species' full geographic distribution. This distribution is the key hedge against major catastrophes that could otherwise extinguish the sole remaining population of a once wide-spread species, as happened to the heath hen (see appendix N). This provision is assured for the spotted owl because regulations pursuant to the National Forest Management Act require it. (It also presents a potential conflict with the guideline below to aggregate available areas into fewer large blocks, as opposed to many small ones.)
- Large blocks of habitat are better than small ones. We agree.
- Problems associated with fragmentation and edge effects (for example, Wilcove et al. 1986) indicate that blocks of contiguous habitat are better than loose aggregations of fragmented blocks. We agree.
- Blocks close together are better than blocks far apart. We agree. The distance between blocks must be well within the known dispersal capability of the species in question.
- Habitat between blocks should be suitable for movement and short stopovers by the species under consideration, to facilitate dispersal of juveniles (and adults) among blocks. We agree (see appendix P).
- The total area available for a reserve system should be divided into as few small blocks as possible (a corollary to "big blocks are better"). We generally agree, but fully implementing this guideline compromises the need to distribute blocks widely over a species' range.

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- Separate habitat blocks should be grouped equidistant from each other, in contrast to a linear distribution. We agree, but the generally linear arrangement of the spotted owl's present geographic distribution imposes limits on our attaining this ideal.
- Habitat blocks should be as nearly circular as possible to minimize dispersal distances within them. This guideline may be true in an unrealistic world without topography and physiography. Realities of terrain and habitat, however, may also influence internal dispersal behavior. For instance, delineation of a single watershed, even if somewhat oblong, may be a superior strategy to a circle. And in a comprehensive set of reserves, occasional linear blocks, strategically situated, might increase the chance of "capturing" birds dispersing from other blocks. Whether this potential benefit would compensate for the lowered efficiency of within-block dispersal, in the long term, is unknown.

In sections that follow, we attempt to develop some of the specifics needed to apply these guidelines. And because the conservation strategy we propose departs so markedly from the one presently in place for spotted owls (the network of SOHAs), we also compare and contrast these alternatives.

Population Size, Density, and Local Extinction

Under present planning guidelines, single pairs of owls are provided for by SOHAs (appendix C). Without exception, empirical studies of the longevity of isolated populations show that those with fewer than two breeding pairs "wink out" (are subject to local extinction) at an unacceptably high rate (recent review in Diamond 1984b). Once stability is reached in the SOHA network (that is, most other available habitat has been made unsuitable for spotted owls, and the remaining population exists in units of one or two pairs), the rate of local extinction will inevitably be too high to assure long-term persistence.

Given that "bigger is better" in terms of habitat area and population size, what is big enough? Because their model did not factor in environmental stochasticity, we disagree with the conclusion by Richter-Dyn and Goel (1972) that, in a population with demographic attributes tending to favor population increase, once a critical population size of about 20 individuals (only 10 pairs) is attained, "extinction is very unlikely" and "expected persistence time immensely long." Empirical data and theoretical modeling indicate, however, that habitat blocks with as few as 15 to 20 pairs have a relatively low probability of winking out (see appendix M). We believe this low probability would hold for a system that includes many such habitat blocks separated by distances and connected by habitat features consistent with the known dispersal tendencies and capabilities of the target species (see appendix P). Indeed, we believe that such an arrangement of large habitat blocks probably functions more like a single, interacting population, than as isolated subpopulations. Haila and Hanski (1984) reached a similar conclusion, suggesting that the effective areas of habitat blocks are increased when birds can move between them with relative ease. Haila and Hanski contend that it may be more appropriate to regard the entire "archipelago" of patches as the habitat block.

Because the size of a population assured by an HCA is among the most important determinants of long-term population maintenance, we have summarized the key studies that examine persistence times in relation to population size.

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Empirical Evidence

Southern (1970)—A study of tawny owls in Wytham Woods, near Oxford, England, began with a population of 17 pairs in 1947, after an unusually severe winter (Southern 1970). The population increased slowly during ensuing years, reaching 30 pairs in 1955 and 31 or 32 pairs in each year thereafter, until the study ended in 1959. Wytham Woods is part of an old estate about 4 miles northwest of Oxford, generally in an area of farmland. We have not been able to determine how far the area is from other subpopulations of tawny owls, however, or how large those subpopulations may be.

Jones et al. (1976)—Jones et al. (1976) reported on bird populations on the Channel Islands, off the coast of southern California, which range from 32 to 157 miles from the mainland. From figure 6 in Jones et al., we estimate that over a period of nearly 100 years of bird surveys there, extinction rates were about 10% for populations of 37 pairs, about 15% for populations of 20 pairs, and about 20% for populations of 12 pairs. These rates of extinction are slightly higher than indicated in the British islands reported in the next three studies below. This difference almost certainly reflects the smaller role of a “rescue effect” (immigrants entering a population at a rate high enough to slow or overcome extinction events—Brown and Kodric-Brown 1977) in the Channel Islands because they are much farther from the mainland than the British islands.

Diamond and May (1977)—A tabulation of bird censuses (Diamond and May 1977) on the Fame Islands (total area 79 acres, situated 3.1 miles from the mainland of Britain) reports on an uninterrupted series of 29 years—1946 to 1974 (28 between-year intervals). Data are given for all species ($n = 16$) of land birds breeding on the islands. Considering the four large-bodied, nonmigrant species (see justification below, in summarization of Pimm et al. 1988), only the ringed plover persisted through the full period of the censuses. Its mean population size was 13 pairs. The moorhen was present as a single pair in 1947 and 1948. The stock dove occurred as a single pair in 1946 and 1972. A single pair of jackdaws was also present in 1949, and two pairs were present in 1964, 1965, and 1966. These findings indicate that a conservation strategy based on single-pair reserves should have limited success in assuring local persistence of a species.

Diamond (1984b)—Diamond (1984b) reported bird censuses over a period of 16 years (1954 to 1969—15 between-year intervals) on Bardsey Island, 445 acres and 3.1 miles from the coast of Britain. Again, looking only at the record for large-bodied, nonmigrant species (table O1), species with mean population sizes of <2 were present in only 3 of 16 years, but all others were present through all 16 years of the study, even those species that have population means of less than five pairs. Several of the species present in all years are capable of lengthy dispersal but are not necessarily inclined to cross a substantial water gap. Consequently, we cannot judge the extent to which persistence of these species resulted from population maintenance on the island, as opposed to rescue by immigrants from the mainland.

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Table O1—Persistence of large-bodied, nonmigrant birds on Bardsey Island from 1954 to 1969 (Diamond 1984b)

Species	Years present	Pairs present			
		Mean ^a	SD	Mm	Max
Sparrowhawk	1954,1955,1956	1.0	0	1	1
Moorhen	All	3.5	2.3	1	8
Ringed plover	1968,1969	1.0	0	1	1
Woodpigeon	1966, 1968, 1969	1.3	0.6	1	2
Little owl	All	4.8	1.3	3	7
Raven	All	2.3	1.5	1	3
Carrion crow	All	4.9	1.2	3	7
Jackdaw	All	30.1	15.9	20	50
Chough	All	2.7	1.0	1	4

^a Means are computed only for years when pairs were present on the island; that is, populations of zero were not considered.

Pimm et al. (1988)—Pimm et al. (1988) give empirical estimates of extinction rates of land birds, using data from consecutive annual censuses of bird populations on 16 islands off the coast of Britain (mean area 0.96 square mile, SD 0.86, range - 0.03 to 3.0; mean distance from mainland = 4.4 miles, SD = 6.9, range = 0.6 to 28). Data from Diamond and May (1977) and Diamond (1984b) were included to generate more robust estimates of times to extinction. Censuses covered many years, and on some islands many decades, to a maximum of 70 years (Pimm, pers. comm.). The shortest set of consecutive censuses covered 13 years and the longest 39 (Diamond and May 1977). Four conclusions apply to the development of a conservation strategy for spotted owls: The rate of extinction is largely explained by mean population size, declining sharply with larger populations; extinction rates are lower for resident birds than for migrants; extinction rates of small and large birds differ significantly; and rates of extinction increase with increasing annual variation in population size.

Because the spotted owl is nonmigratory over most of its range in Washington, Oregon, and northern California, and because it is a large-bodied species by the criteria of Pimm et al., we have used the appropriate subset of their data for our analyses.

Based on our own analyses of those data, a linear regression model best described the relation between population size and persistence in the British data (table O2). For a large-bodied, nonmigratory bird species, the model indicates an average persistence time of 2 years for populations with fewer than 2 pairs, about 25 years for a population of 10 pairs, and about 50 years for one of 20 pairs (table O3).

Another way to look at the data is through the frequency of recorded extinctions in relation to mean population size (table O4). Note that 76% of populations with fewer than 2 pairs became extinct in the study period; 40% of populations including 2 to 5 pairs did so; 21% of nine populations of 6 to 10 pairs became extinct; and none of the seven populations with 11 to 16 pairs did so.

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Table O2—Three regression models describing results in Pimm et al. (1988) from studies of extinction events on 16 islands around Britain (pertains only to large-bodied, nonmigrant birds)

Model	Regression equation	Probability
Linear	$T = -0.56 + 2.54N$	0.008
Log-transformation of persistence time	$T = 3.86e^{0.174N}$	0.023
Second-degree polynomial	$T = 2.16 + 0.97N + 0.11N^2$	0.013

Table O3—Projected extinction times (years) from models in the previous table, in relation to mean population size for large-bodied, nonmigrant birds

Model	Mean population size						
	1	3	5	7	10	15	20
Linear	2	7	12	17	25	38	50
Log-transformation of persistence time	5	7	9	13	22	52	125
Second-degree polynomial	3	6	10	14	23	41	66

Table O4—Extinction rate as a function of mean population size in large-bodied, nonmigrant birds (based on data in Pimm et al. 1988)

Number of pairs	Number of cases	Number of extinctions	Percent
<2	42	32	76.2
2-5+	37	15	40.5
6-10+	9	2	22.2
11-15+	5	0	0.0
16	2	0	0.0

These estimates came from true islands separated from the mainland by water, so dispersal of land birds from the mainland might occur at a lower frequency than dispersal between two mainland “islands” of habitat with patches and stringers of suitable movement cover between them (as would be true for a set of HCAs for spotted owls). On the other hand, the mean distance of the islands from the mainland in the study by Pimm et al. was only 4.2 miles, and six of the islands were within 1.2 miles of the mainland. These distances probably do not constitute a barrier for many species of land birds. The rescue effect probably plays a significant role in the dynamics of the British island situation. Whether these data overestimate or underestimate the true rate of extinction of large-bodied, nonmigrant birds from island habitats, they are among the best data available on this question.

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Walter (unpubl. ms.)—On Socorro Island, about 285 miles SSE of the southern tip of Baja California, the Socorro island red-tailed hawk population has numbered between 15 and 25 pairs per year for the past 20 to 25 years (Walter, unpubl. ms.; also see Jehl and Parkes 1982). Walter believes that the population is at or near carrying capacity, so its numbers have probably not been much greater at any time in recent history.

Significantly, the Socorro Island hawks are sufficiently distinct from mainland populations of red-tailed hawks to be described as an endemic subspecies (see Friedmann 1950). It is markedly melanistic, although not distinctly so from a mainland subspecies, but it has distinctly more robust legs and feet (Jehl and Parkes 1982). Although this differentiation may have resulted from the founder effect, it nonetheless suggests a long tenure of this population on Socorro Island. This example is not offered as evidence that such small populations can routinely be expected to persist for decades or centuries. We agree with Walter (unpubl. ms.) that this is not generally true. But this population has apparently survived a genetic bottleneck and persisted for a long time, with an average population size of about 20 pairs.

Dennis et al. (unpubl. ms.)—Other examples of small populations without access to rescue effects, but which have persisted for long periods of time, are reported by Dennis et al. (unpubl. ms.). For example, the whooping crane population in North America was estimated at 18 birds in 1938. The population fluctuated about that number for nearly 2 decades, when it slowly began to increase in the early 1960s. This preceded serious conservation efforts to save whooping cranes. Puerto Rican parrots numbered in the low 20s in 1968, declined to fewer than 15 birds in the early 1970s, and then slowly began to increase during the early 1980s, in response to heroic conservation efforts. (We have not yet learned of the full effect of a recent hurricane on Puerto Rican parrots, but the incident emphasizes our concern for spreading the risk by distributing a species widely throughout its range.) As with the Socorro Island red-tailed hawk, we consider these cases anomalous. Were either of these species' populations fortified by other subpopulations with which they could interact demographically, the outlook for both species would undoubtedly be brighter.

Ganey and Fletcher (pers. comm.)—Many populations of spotted owls in Arizona and New Mexico occur in relatively isolated mountain ranges, sometimes separated by wide expanses of Sonoran desert or other nonforested lands. Excerpts from a letter from Ganey (14 February 1990) follow: "The distributional pattern of spotted owls in southern Arizona remains incompletely known, the extent of suitable habitat per mountain island is unknown, and densities in different islands of habitat are unknown. What is clear about this region is that spotted owls are widely distributed throughout these mountain islands. Some...are large, appear to contain lots of suitable habitat, and probably support populations of greater than 30 pairs each. Others are relatively small, and probably support only a few pairs. It is hard to envision stable, self-supporting populations in some of the smaller ranges. Therefore, I believe that dispersal must occur between these islands, although this has not been documented...Spotted owls may also find the lowlands between islands less hostile than I once thought. In recent years...[we have obtained] a number of verified occurrences of owls in these lowlands between November and April."

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We can draw only limited inferences from the spotted owl situation in the Southwest. First, we lack good data on population sizes and the distances between populations. Second, the spotted owl in Arizona and New Mexico is a different subspecies that has evolved in a different milieu from that in the conifer forests of the Pacific Northwest. The dispersal behavior of the northern spotted owl evolved over millennia in relatively continuous expanses of conifer forest. The Mexican spotted owl evolved in a landscape containing massive visual cues to the locations of suitable habitat—mountain tops. But at least this case shows that one subspecies of spotted owls can maintain relatively small subpopulations in isolated mountain ranges, probably through rescue effects from larger populations many miles distant.

Modeling Results

Shaffer and Samson (1985)—Setting an arbitrary criterion of 95% probability of persistence of the Yellowstone grizzly bear population for 100 years, Shaffer and Samson (1985) ran 50 simulations of population persistence for 100 years. They used “a discrete time, discrete number formulation employing the sex and age structure, mortality and reproductive rates, and density-dependent relationships” from an independent study by Craighead et al. (1974) with 12 years of data on grizzly bears in Yellowstone. Environmental and demographic stochasticity were introduced into the model.

Because the model assumed a homogeneous habitat—that is, no barriers to dispersal—and did not attempt to deal with catastrophes, it probably underestimates the probability of extinction. On the other hand, the model assumed a closed population, precluding a rescue effect. Populations benefiting from rescue effects would be expected to have lower extinction rates than those indicated by Shaffer and Samson’s model. How these various factors would balance out is anyone’s guess at this time. We present results of the grizzly bear models, however, as part of the information considered to arrive at a decision about the number of pairs needed in individual HCAs for spotted owls.

All 50 initial populations of 10 individual grizzly bears became extinct within 100 years, 32 populations of 20 individuals became extinct, 13 populations of 30, 3 populations of 40, and 1 population of 50 initial populations of 50 individuals became extinct. These results suggest that some number of grizzly bear pairs between 20 and 25 met the criterion of 95% confidence that a population would still be extant after 100 years.

Lamberson et al. (unpubl.) and additional modeling by our team—Details of simulations by Lamberson et al. (unpubl.) are given in appendix M (especially see figs. M15, M16, and M17). Model parameters were based on estimated vital rates of the northern subspecies, integrated spatial distribution of blocks of habitat, dispersal parameters believed to be reasonable for spotted owls, and demographic and environmental stochasticity. Hundreds of simulation runs suggest that a system of HCAs containing somewhere between 15 and 20 pairs, with moderately effective between-block dispersal, shows marked persistence over a 100-year simulation period.

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Dispersal

The study by Soulé et al. (1988), briefly described above, emphasized the critical need for a conservation plan to assure that the species be able to move readily among blocks of suitable habitat. Without the availability of dispersal routes, populations supported by habitat blocks must be self-sustaining—an unlikely event in all but exceptionally large blocks that are capable of sustaining very large populations. The current management plan for spotted owls on Federal lands in Washington, Oregon, and California is based on a “network” of SOHAs, each intended to provide sufficient habitat for a single pair of owls to survive and reproduce (although some SOHAs may, in fact, provide for more than one pair—probably rarely more than two). SOHAs are dispersed across landscapes of National Forests and BLM Districts at distances typically ranging from 8 to 12 miles. This spacing assumes that dispersing juveniles (or displaced adults) will be able to locate suitable habitat for breeding in SOHAs vacated by death or emigration of former residents. The SOHA network has been widely criticized by conservation biologists as inadequate, but before suggesting an alternative approach we need to evaluate whether the network system is flawed in terms of dispersal. We believe it is, for at least two reasons.

First, as the SOHA system stabilizes (that is, as the surrounding landscape matrix is converted to younger-aged forests), spotted owls will be required to disperse across increasingly longer gaps of unsuitable or marginally suitable habitat. This decrease in the quality of this matrix makes it more and more imperative that dispersing owls quickly locate a SOHA. Second, we believe isolated SOHAs will markedly reduce the ability of dispersing individuals to locate suitable mates (the Allee effect). If the SOHA already has a breeding pair, a newcomer will not be able to establish a breeding territory there. If it has only one spotted owl in it when the newcomer arrives, that owl must be of the opposite sex for any chance of the newcomers settling to breed. And if the SOHA is unoccupied when the newcomer arrives, it may be a long time before another newcomer of the opposite sex finds the same SOHA.

A system of HCAs has at least three dispersal advantages over SOHAs. First, it provides for turnover events based on internal recruitment and dispersal within each HCA (related to the point on floaters, below). We already know that this phenomenon occurs in relatively large, continuous populations of spotted owls (Franklin et al. 1989). Second, it enhances dispersal between HCAs because the very size of an HCA makes it more likely to be “hit” by a bird dispersing from another locality (see discussion of this point in Diamond 1984b). Furthermore, some purposeful arrangement of HCAs can be implemented to increase the likelihood of a dispersing bird encountering it, such as arranging oblong HCAs with their long dimension extending a substantial distance east-to-west or north-to-south. Third, if spotted owls tend to vocalize more frequently when in relatively dense populations than when isolated from other pairs, and if dispersing birds respond to calls of other owls to help guide them to suitable habitat, HCAs are more likely than isolated SOHAs to attract dispersers.

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Pertinent vocalization phenomena have been shown in several bird species. Boag (1976) reported that “the establishment of ruffed grouse territories is not entirely in response to availability of potentially acceptable vegetation.” His results suggested a “form of social interaction between established and establishing birds.” With increased clumping of birds on perennial sites, yet more birds were attracted, leading to higher drumming rates, so that social interaction within the population increased with density. Similarly, Gochfeld (1978) found that the number of flight songs per male per minute was linearly related to group size in the pampas meadowlark. Kroodsma and Vemer (1978) found that sedge wrens sang at a higher rate, and for a greater percentage of the time when a neighbor was singing, than when the neighbor was silent. Such behavior, called “countersinging,” is widespread among birds. The result tends to be a self-accelerating generation of active vocalization by members of a population, as the songs and calls effectively enlarge the “detectable boundary” of a suitable habitat patch for birds seeking a potential territory. This added detectable boundary is equal to the audible range of the songs and calls produced. Such cues will be produced more continuously by a group than by a single bird or pair of birds, increasing the likelihood that a searching bird passing by will hear a cue. Although vocal cues of this sort do not assure that a searching bird will find an unoccupied territory, we believe they increase that chance.

The benefits of this auditory effect are minimal at best in a system of SOHAs capable of supporting single pairs. Only if an owl is established in a SOHA will calling have any chance of attracting another bird, because calls obviously will not emanate from vacant SOHAs capable of supporting only a single pair of birds. The irony is that an available but empty SOHA will lack any kind of vocal cue to its location.

Fragmentation and Edge Effects

Fragmentation and edge effects are a major concern for species threatened with the systematic removal of suitable habitat (see appendix N). Present evidence convinces us that fragmentation of homogeneous forest tracts tends to be accompanied by lowered spotted owl densities (see, for example, appendix H). It also increases the vulnerability of remaining stands to windstorms. The relatively small size of SOHAs results in a high ratio of edge to habitat area, worsening problems of fragmentation and edge effects. But even more serious is the fact that SOHAs are themselves internally fragmented into smaller blocks of suitable habitat that further increase the ratio of edge to area. This condition would increase all detrimental effects of fragmentation, and might increase competition with barred owls and predation by great horned owls (see section on competition and predation, below; also appendix N).

On the other hand, HCAs, unfragmented by timber harvesting, would provide a significant hedge against fragmentation effects, at least at a scale of several square miles. Of course the full benefit will not be realized until already fragmented forests in proposed HCAs have regenerated.

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Predation and Interspecific Competition

The issues of predation on spotted owls, especially by great horned owls, and interspecific competition with barred owls, have surfaced repeatedly during the past decade or so (review in Hamer 1989). In each case, the expressed concern is that fragmentation, and the increasing extent of edges, favor the great horned and barred owls, and probably bring them into closer contact with spotted owls. Although these concerns have not been substantiated (see Hamer 1989), neither is easily researched. If either or both of them do have substance, however, the creation of large blocks of habitat as envisioned in the HCAs should lessen the effects of fragmentation and edges on spotted owls compared to SOHAs.

Catastrophes

Catastrophes come in different sizes, as for example in the form of local to wide-spread droughts, small fires to major conflagrations, localized high winds to extensive and powerful storms, and so on. Habitat Conservation Areas offer some cushion against smaller, more localized catastrophes (see appendix N). Small fires, for example, could easily destroy entire SOHAs, or reduce the amount of suitable habitat in them to a point that they could no longer support a breeding pair of owls. Fires of the same size would have relatively little impact on an HCA of many square miles. We further believe that SOHAs, as presently configured with multiple patches of relatively small stands of forest, are particularly vulnerable to windstorms.

Careful planning and certain kinds of management within HCAs can lessen the negative consequences from events such as fire, insect infestations, and forest-tree diseases. We expect that certain types and intensities of prescribed fire fit that category. Elsewhere (appendix Q), we recommend the development of plans to reduce potential hazards from such events to HCAs. This recommendation is not a license to optimize planning for hazard reduction without regard for the needs of spotted owls within HCAs. But we do believe that opportunities exist to reduce such hazards without compromising the habitat value of HCAs for the owls.

Major catastrophes like the 1921 hurricane on the Olympic Peninsula, the extensive “Columbus Day storm” in Oregon in 1962, and the 1987 fires in California will affect extensive areas of the landscape regardless of HCA size. Local conservation planning cannot cope with the geographic scale of such catastrophes. Our hedge against such events causing regional extinction of the spotted owl is the widespread geographic distribution of HCAs recommended in this plan. Short of region-wide effects, such as a prolonged drought or global warming, major catastrophes tend to be on a scale that might destroy all or part of a single HCA or a number of SOHAs established in the same landscape. To that extent, the HCA system proposed here and the SOHA network system offer about the same amount of protection from major catastrophes. We can envision no system that is totally immune to major catastrophic events. We cannot control them, and we cannot guarantee security from them in any given conservation strategy that might be contrived for spotted owls.

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Providing for Floaters

Floaters are nonterritorial, nonbreeding birds generally considered surplus individuals or population reserves (Brown 1969). Their occurrence and dynamics are unquestionably among the most intractable aspects of avian ecology to study, because floaters in most species tend to remain silent and inconspicuous. Nonetheless, their existence among bird species is probably widespread in most or all populations at carrying capacity (for example, see Hensley and Cope 1951; Knapton and Krebs 1974; Krebs 1971; Rappole et al. 1977; Smith 1978, 1984; and Stewart and Aldrich 1951). Smith (pers. comm.) explains that floaters generally exhibit one of two divergent strategies. They form groups in suboptimal habitat (like the well-known case in red-winged blackbirds, Orians 1961) “...or they live singly and spend at least some time in areas defended as territories by owners. Owls would **doubtless** [sic] follow the latter strategy” (Smith, pers. comm.). Although no clear information is available on floaters in the northern spotted owl, studies of banded birds strongly suggest their presence (Forsman, pers. comm.; Franklin, pers. comm.)

The most intensive study of the general strategy, which Smith (pers. comm.) believes holds true for floaters in spotted owl populations, was undertaken in a population of rufous-collared sparrows in Costa Rica (Smith 1978). There, floaters “did not wander randomly; rather, they lived in well-defined, restricted home ranges within other birds’ territories. Female home ranges were usually single territories; male ranges, usually three to four territories. Since range limits of both sexes coincide with territory boundaries, the net effect is two unique single-sex dominance hierarchies of floaters for each territory. When an owner dies, it is nearly always replaced very quickly by the dominant local [floater] bird of the appropriate sex.” In a study of winter flocks of black-capped chickadees in Massachusetts, Smith (1984) reported similar dynamics among floaters. About 80% of the population remained in flocks with fixed home ranges, but 20% of the birds switched regularly among flocks. The surprising result was that when a high-ranking flock member disappeared during the winter, it was rapidly replaced by the dominant local floater of the appropriate sex—not by the next ranked regular flock member. Smith (1984) contends that “the many similarities between chickadee flock switchers and [floaters among] rufous-collared sparrows suggest that complex organization among floaters may be widespread” among birds.

The HCAs proposed in this conservation strategy are more likely than SOHAs to include areas where floaters can persist, and these then serve as ready sources of replacements for birds that die or vacate their territories for other reasons (see comments on dispersal, above). We see little or no opportunity for such dynamics among floaters in single SOHAs. Indeed, we doubt that the SOHA system, when fully stabilized, would provide for floaters at all. In any event, if floaters are not integrated into populations of breeders, the rate at which deceased breeders are replaced by floaters would surely be significantly less than the rate in an HCA with many breeding pairs.

Number of Owls in Relation to the Amount of Suitable Habitat

Single SOHAs need to provide sufficient suitable habitat for a single pair to breed successfully on a sustained basis. But isolated SOHAs cannot take advantage of the fact that neighboring owl pairs commonly share substantial portions of their home ranges. As a result, large HCAs should support more owl pairs in a given amount of suitable habitat than will numerous SOHAs that add up to the same amount.

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Social Facilitation

Social facilitation refers to the positive effects of interaction among animals in a population. Some studies (see Collias 1971) indicate that these effects markedly increase the likelihood, frequency, and success of pair bonding in birds. A manifestation of this effect, referred to in the above section on dispersal, is increased singing activity in a neighborhood of territorial male birds. If such a phenomenon plays a role in the breeding biology of spotted owls, it will be more effective in an HCA that includes many pairs than in an isolated SOHA with only one or two pairs.

Monitoring

We believe a strategy based on numerous, relatively large HCAs is amenable to a better and no more costly monitoring system than the one currently being used to monitor spotted owl occupancy in SOHAs (see appendix R). Start-up costs may be higher, however, to accomplish full inventories of spotted owls in the HCAs.

Implementation

For several reasons, the arrangement of HCAs proposed in this plan would be markedly less complex to implement and manage than the current network of SOHAs. First, many fewer units are required and their large sizes allow better assessment of impacts and require less record-keeping to track them through time. Second, their boundaries can be more precisely delineated than those of SOHAs because they will not be subject to the timber-harvest activities that have created fragmented patches of suitable habitats in SOHAs. Third, standards and guides for HCAs will be simpler because future timber harvest will be excluded within their boundaries.

Possible Advantages of SOHAs Over HCAs

The distribution and arrangement of HCAs proposed in this plan will reduce one aspect of the well-distributed pattern of SOHAs in the current management scenario. On the one hand, at least in the short term, we expect the number of owl pairs now in the landscape matrix surrounding proposed HCAs to decline in abundance as the forest in that region is reduced. On the other hand, the total distribution of owls on a geographic scale should remain unchanged in the short term and should improve over the long term, as proposed HCAs (such as those in the Oregon Coast Range) develop forest conditions capable of supporting breeding owl populations. Furthermore, we believe that more owl pairs will be protected in proposed HCAs in the short term than the number now believed to be protected by SOHAs, and many more will be protected by HCAs in the long term (see appendix Q). On balance, the potential negative impacts of losing owls in areas between HCAs are most likely outweighed, by at least one order of magnitude, by the increased stability of populations within the HCAs.

We believe that most effects of increased owl density in the HCAs will have largely positive effects on population persistence, even though the potential rate of disease transmission is higher where more animals come into contact more frequently (Simberloff and Abele 1976a). We agree with Diamond (1976) that disease transmission is a trivial concern when weighed against the many advantages previously summarized. Predation might also increase in an area of higher density, but only if a given predator begins to specialize on spotted owls as a prey source. We consider this unlikely, given the fact that great horned owls and goshawks are probably the only species that occasionally prey on spotted owls. Goshawks tend to be prey generalists, taking a wide variety of birds; great horned owls prey more on mammals than on birds. In fact, we are more concerned about the likelihood that predation by great horned owls will increase in areas where the forest has been removed or thinned, because great horned owls are thought to be more abundant in less densely

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forested habitats. As discussed previously, spotted owls are probably more secure from predation by great horned owls in undisturbed forests, especially those with multiple layers, where they have a better chance to outmaneuver an attacking great horned owl.

If a major catastrophic event should destroy an entire HCA, more pairs of owls would be lost than if the area had contained only widely dispersed SOHAs (see Simberloff and Abele 1976a). In either case, however, the event would create a worrisome increase in distance that owls would need to cross when dispersing through the area. We believe this disadvantage is more acute with SOHAs than with a system of larger HCAs. Again, the major advantage of having relatively stable breeding units in HCAs, in contrast to the highly extinction-prone SOHAs, far outweighs any potential advantage that SOHAs may offer in the event of a major catastrophe. Furthermore, as explained previously, SOHAs are much more vulnerable than large HCAs to complete destruction by smaller catastrophes at smaller geographic scales, which occur much more often than major ones.

Because proposed distances between HCAs are sometimes greater than distances between SOHAs, mammalian prey species of the spotted owl may not disperse as readily between them. First, we believe this would not happen, because the HCAs would be large enough that a dispersing small mammal would more likely encounter them than one of the few SOHAs scattered over the same area. Second, the proposed HCAs will be large enough to support viable populations of prey species. For example, studies indicate densities of flying squirrels of about one to two per acre (Carey, pers. comm.). Even a SOHA could be expected to have populations of a few thousand flying squirrels. Our proposed HCAs should have self-sustaining populations of all prey species taken frequently by spotted owls. We do not envision a crucial role for the rescue effect in maintaining these prey populations.

References

- Boag, D. A. 1976.** Influence of changing grouse density and forest attributes on the occupancy of a series of potential territories by male ruffed grouse. *Can. J. Zool.* 54:1727-1736.
- Brown, J. H., and A. Kodric-Brown. 1977.** Turnover rates in insular biogeography: Effect of immigration on extinction. *Ecology* 58:445-449.
- Brown, J. I. 1969.** Territorial behavior and population regulation in birds. *Wilson Bull.* 81:293-329.
- Carey, A. B. 1989. Pers. comm.** U.S. For. Serv., PNW, Olympia, Wash.
- Collias, N. E., J. K. Victoria, and R. J. Shallenberger. 1971.** Social facilitation in weaverbirds: Importance of colony size. *Ecology* 52:823-828.
- Craighead, J. J., J. B. Varner, and F. C. Craighead, Jr. 1974.** A population analysis of the Yellowstone grizzly bears. *Bull. 40. Montana Forest Conserv. Exp. Stn., Univ. Montana, Missoula.*
- Den Boer, P. J. 1981.** On the survival of populations in a heterogeneous and variable environment. *Oecologia* 50:39-53.

Appendix O: HCA Size and Spacing

- Dennis, B., P. L. Munholland, and J. M. Scott. Unpubl. ms.** Estimation of growth and extinction parameters for endangered species. Univ. Idaho, Moscow, and Montana State Univ., Bozeman. Typescript.
- Diamond, J. M. 1975.** The island dilemma: Lessons of modern biogeographic studies for the design of natural reserves. *Biol. Conserv.* 7:129-146.
- Diamond, J. M. 1976.** Island biogeography and conservation: Strategy and limitations. *Science* 193:1027-1029.
- Diamond, J. M. 1984a.** Distributions of New Zealand birds on real and virtual islands. *New Zealand J. Ecol.* 7:37-55.
- Diamond, J. M. 1984b.** "Normal" extinctions of isolated populations. Pages 191-246 in M. H. Nitecki, ed. *Extinctions*. Univ. Chicago Press, Chicago.
- Diamond, J. M., K. D. Bishop, and S. van Balen. 1987.** Bird survival in an isolated Javan woodland: Island or mirror? *Conserv. Biol.* 1:132-142.
- Diamond, J. M., and R. M. May. 1977.** Species turnover rates on islands: Dependence on census interval. *Science* 197:266-270.
- Fletcher, K. W. Pers. comm.** U.S. For. Serv., Albuquerque, N. Mex.
- Forman, R. T. T., A. E. Gaul, and C. F. Lock. 1976.** Forest size and avian diversity in New Jersey woodlots with some land use implications. *Oecologia* 26:1-28.
- Franklin, A. B., J. A. Blakesley, and R. J. Gutiérrez. 1989 unpubl.** Population ecology of the northern spotted owl (*Strix occidentalis caurina*) in northwest California: Preliminary results, 1988. Report to the California Department of Fish and Game. Typescript.
- Friedmann, H. 1950.** The birds of North and Middle America. Vol. 11, Pt. II. U.S. Natl. Mus. Bull. 50. U.S. Gov. Print. Off., Washington, D.C. 793pp.
- Ganey, J. L. Pers. comm.** N. Ariz. Univ., Flagstaff.
- Halla, Y., and I. K. Hanski. 1984.** Methodology for studying the effect of habitat fragmentation on land birds. *Annales Zoologici Fennici* 21:393-397.
- Harris, L. 1984.** The fragmented forest. Univ. Chicago Press, Chicago. 211pp.
- Hensley, M. M., and J. B. Cope. 1951.** Further data on removal and repopulation of the breeding birds in a spruce-fir community. *Auk* 68:483-493.
- Gochfeld, M. 1978.** Social facilitation of singing, group size, and flight song rates in the pampas meadowlark *Sturnella defilippii*. *Ibis* 120:338-339.
- Griffith, B., J. M. Scott, J. W. Carpenter, and C. Reed. 1989.** Translocation as a species conservation tool: Status and strategy. *Science* 245:477-480.

Appendix O: HCA Size and Spacing

- Jehl, J. R., and K. C. Parkes. 1982.** The status of the avifauna of the Revillagigedo Islands, Mexico. *Wilson Bull.* 94:1-19.
- Jones, H. L., and J. M. Diamond. 1976.** Short-time-base studies of turnover in breeding bird populations on the California Channel Islands. *Condor* 78:526-549.
- Karr, J. R. 1982.** Avian extinction on Barro Colorado Island, Panama: A reassessment. *Am. Nat.* 119:220-239.
- Knapp, R. W., and J. R. Krebs. 1974.** Settlement patterns, territory size, and breeding density in the song sparrow (*Melospiza melodia*). *Can. J. Zool.* 52:1413-1420.
- Krebs, J. R. 1971.** Territory and breeding density in the great tit *Parus major* L. *Ecology* 52:2-22.
- Kroodsma, D. E., and J. Verner. 1978.** Complex singing behaviors among *Cistothorus* wrens. *Auk* 95:703-716.
- Lamberson, R. H., R. McKelvey, B. R. Noon, and C. Voss. Unpubl. ms.** The effects of varying dispersal capabilities on the population dynamics of the northern spotted owl—prelim. results.
- Lovejoy, T. E., J. M. Rankin, R. O. Bierregaard, K. S. Brown, L. H. Emmons, and M. E. Van der Voort. 1984.** Ecosystem decay of Amazon forest remnants. Pages 295-325 in M. H. Nitecki, ed. *Extinctions*. Univ. Chicago Press, Chicago.
- Noss, R. F., and L. D. Harris. 1986.** Nodes, networks, and MUMs: Preserving diversity at all scales. *Environ. Manage.* 10:299-309.
- Orlans, G. H. 1961.** The ecology of blackbird (*Agelaius*) social systems. *Ecol. Monogr.* 31:285-312.
- Pimm, S. L., H. L. Jones, and J. Diamond. 1988.** On the risk of extinction. *Am. Nat.* 132:757-785.
- Pimm, S. L. Pers. comm.** Univ. Tenn., Knoxville.
- Rappole, J. H., D. W. Warner, and M. Ramos. 1977.** Territoriality and population structure in a small passerine community. *Am. Mid. Nat.* 97:110-119.
- Richter-Dyn, N., and N. S. Goel. 1972.** On the extinction of a colonizing species. *Theor. Popul. Biol.* 3:406-433.
- Scott, J. M., C. B. Kepler, C. van Riper III, and S. I. Fefer. 1988.** Conservation of Hawaii's vanishing avifauna. *BioScience* 38:238-253.
- Shaffer, M. L., and F. B. Samson. 1985.** Population size and extinction: A note on determining critical population sizes. *Am. Nat.* 125:144-152.

Appendix O: HCA Size and Spacing

- Simberloff, D., and L. G. Abele. 1976a.** Island biogeography theory and conservation practice. *Science* 191:285-287.
- Simberloff, D., and L. G. Abele. 1976b.** Island biogeography and conservation: Strategy and limitations. *Science* 193:1032.
- Simberloff, D., and L. G. Abele. 1982.** Refuge design and island biogeographic theory: Effects of fragmentation. *Am. Nat.* 120:41-50.
- Smith, S. M. 1978.** The “underworld” in a territorial sparrow: Adaptive strategy for floaters. *Am. Nat.* 112:571-582.
- Smith, S. M. 1984.** Flock switching in chickadees: Why be a winter floater? *Am. Nat.* 12:81-98.
- Smith, S. M. Pers. comm.** Mount Holyoke Coll., South Hadley, Mass.
- Soulé, M. E., D. T. Bolgor, A. C. Alberts, J. Wright, M. Sorice, and S. Hill. 1988.** Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. *Conserv. Biol.* 2:75-92.
- Southern, H. N. 1970.** The natural control of a population of tawny owls (*Strix aluco*). *J. Zool. London* 162:197-285.
- Stewart, R. E., and J. W. Aldrich. 1951.** Removal and repopulation of breeding birds in a spruce-fir community. *Auk* 68:471-482.
- Terborgh, J. 1976.** Island biogeography and conservation: Strategy and limitations. *Science* 193:1029-1030.
- Vuilleumier, F. 1970.** Insular biogeography in continental regions. I. The northern Andes of South America. *Am. Nat.* 104:373-388.
- Walter, H. L. Unpubl. ms.** Small viable population: The red-tailed hawk of Socorro Island. Typescript.
- Whitcomb, R. F., J. F. Lynch, P. A. Opler, and C. S. Robbins. 1976.** Island biogeography and conservation: Strategy and limitations. *Science* 193:1030-1032.
- Whitcomb, R. F., C. S. Robbins, J. F. Lynch, B. L. Whitcomb, M. K. Klimkiewicz, and D. Bystrak. 1981.** Effects of forest fragmentation on avifauna of eastern deciduous forest. Pages 125-205 in R. L. Burgess and D. M. Sharpe, eds. *Forest island dynamics in man-dominated landscapes*. Springer Publishing Co., New York.
- Wiens, J. A. 1989.** The ecology of bird communities, Vol. 2: Processes and variations. Cambridge Univ. Press, Cambridge. 316pp.

Appendix O: HCA Size and Spacing

- Wilcove, D. S., C. H. McLellan, and A. P. Dobson. 1986.** Habitat fragmentation in the temperate zone. Pages 237-256 *in* M. Soulé and B. A. Wilcox, eds. Conservation biology: The science of scarcity and diversity. Sinauer Associates, Sunderland, Mass.
- Williams, G. R. 1981.** Aspects of avian island biogeography in New Zealand. *J. Biogeogr.* 8:439-456.
- Willis, E. O. 1974.** Populations and local extinctions of birds on Barro Colorado Island, Panama. *Ecol. Monogr.* 44:153-169.
- Willis, E. O. 1980.** Species reduction in remanescent woodlots in southern Brazil. Pages 783-786 *in* R. Höhring, ed. Acta 19th Congressus Internationalis Ornithological, Vol. 2. Deutsche Ornithoigen-Gesellschaft, Berlin.

Connectivity: Assuring Successful Dispersal

Introduction

Elsewhere, we emphasized the vital need to assure that spotted owls can move with at least moderate success from one HCA to another (appendices M, N, O, and P). Here, we develop more fully the concepts of dispersal and connectivity that are involved in this process, and apply the relevant information now available on spotted owls to assure this movement.

Dispersal

Dispersal in animals can be defined as the relatively permanent movement of individuals from one location to another. Usually dispersal is the movement of juveniles from their natal area to a site where they eventually settle to breed. Occasionally, adults disperse from one breeding site to another, typically in response to a disturbance in their former breeding area. The regular migratory movement of birds between breeding and nonbreeding areas is not dispersal. Although habitat destruction is probably the main reason for breeding adults to disperse in search of another breeding area, other factors may also induce adult dispersal. Successful dispersal is an essential feature of a conservation strategy: without it, deceased individuals in the breeding population will not be replaced by recruits among dispersing juveniles and displaced adults, and the population will decline to extinction.

Consensus exists among biologists that, all else being equal, continuous suitable habitat supports more individuals of a species targeted for conservation than does fragmented (discontinuous) habitat. Persistence times for populations that inhabit fragmented landscapes are thought to be greater where connectivity between habitats enhances the exchange of individuals. With that in mind, much recent literature in conservation biology supports the concept of providing “corridors” of suitable habitat between population centers (for example, Diamond 1975, Harris 1984, Noss and Harris 1986, Soulé et al. 1988, Terborgh 1975, Willis 1974, Wilson and Willis 1975). Evidence is scanty, however, on exactly what kind of corridors each particular species requires, and some authors suggest that attempts to provide corridors may sometimes turn out to be more detrimental than beneficial (see Noss 1987, Simberloff and Cox 1987, Soulé and Simberloff 1986). When large blocks of suitable habitat for a species exist, however, the rate of successful dispersal from one block to another clearly declines with increasing distance between them (see Diamond 1975, Gilpin and Diamond 1976, and appendix O). Our own modeling efforts indicate that long-term spotted owl persistence is unusually sensitive to the distance between blocks of suitable habitat in relation to the percentage of the landscape that a dispersing

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individual can search before perishing (appendix M). As Miller (1989:1-2) states, “The distance between adjacent pairs or groups of breeding owls should be such that dispersal of juveniles can replace losses (deaths or emigrations) among existing pairs and provide for the colonization of suitable, unoccupied habitats. An understanding of dispersal in juvenile spotted owls is thus basic to formulation of criteria for appropriate spacing of habitat to accommodate owl pairs.”

The habitat conservation strategy proposed here does not depend on specific corridors for dispersal of the northern spotted owl. Instead, we provide recommendations for managing the landscape to facilitate movement of owls between HCAs. Here we address the essential elements of suitable spotted owl connectivity between HCAs. The following data on the dispersal capabilities of spotted owls, and the nature of connecting zones between HCAs, support plan guidelines.

Observations on Dispersing Juveniles

Miller (1989) carried out the most extensive study to date, monitoring dispersing juveniles over a 4-year period. He reported that 32 of 48 juveniles in western Oregon, fitted with radio transmitters shortly after leaving their nest, survived to disperse from the natal areas (an average of 104 days after fledging). Twenty-seven (84%) initiated dispersal between mid-September and mid-October. Their initial movement was usually rapid, and “...most juveniles settled into well-defined areas for their first winter after the initial dispersal movements. Those...surviving their first winter often began moving again in late winter or early spring.” Males dispersed an average of 16.2 miles (SD = 14.6; $n = 7$) and females an average of 20.4 (SD = 6.6; $n = 6$, not significantly different), from a subset of birds positively identified to sex. Directions taken by dispersing juveniles did not differ from a random distribution, although six of nine juveniles in 1983 dispersed down the McKenzie River drainage from the H.J. Andrews Experimental Forest. Miller found no significant relation between forest fragmentation and either the final distance moved or the number of days survived by birds in his study. Dispersing juveniles used a wide variety of habitats, but 12 of 18 birds exhibited significant selection for old-growth and mature forests.

In a study of 23 dispersing juveniles in northwestern California (11 in 1983 and 12 in 1984), Gutiérrez et al. (1985) reported departure dates from natal areas from 22 September to 5 October. These dates were within the range of those reported by Miller (1989) for western Oregon. In 1983, dispersing juveniles moved an average of 5 miles per day (range 1 to 11), compared to just 1.3 miles per day in 1984 (range 0.8 to 6.4). The difference was statistically significant. Directions taken by dispersing birds varied. Gutiérrez et al. found no relation between “...dispersal direction and the geographic orientation of drainages or ridges.” During the first 80 days of dispersal, individual juveniles in this study dispersed total distances from 15.3 to 92.9 miles ($n = 11$) in 1983, and from 0.7 to 62.8 miles ($n = 7$) in 1984. Total distance is the sum of all segments between successive locations as birds were followed during dispersal. Total distance is greater than the straight-line distance between beginning and ending points.

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Estimating Dispersal Distances

In addition to these more extensive radio-transmitter studies of dispersing juveniles, we have compiled results from all sources into a data base used to estimate dispersal distances of juvenile spotted owls after they leave their natal areas (table P1). We have also compiled a smaller data set from known dispersal distances of color-banded juveniles (table P2). Both data sets have limitations. Radio-transmitter studies usually allowed observers to relocate birds at regular intervals until the transmitters failed or the birds disappeared or died. Consequently, the results were not constrained by any boundaries within which searching occurred. Only one bird from the collected surveys was later found to be paired with a mate on a territory, although it apparently never nested (Gutiérrez, pers. comm.). All other birds ($n = 55$) either died (68%), their transmitters failed (27%), or they disappeared (5%). Although juvenile birds of all species tend to have high mortality rates, results from the radio-marked birds may be biased by the possible effects of radio-transmitters.

Table P1—Number of radio-marked juveniles that dispersed different distances (intervals grouped by miles) (from Forsman 1980, Gutiérrez et al. 1985, Laymon 1988, Meslow and Miller 1986, and Miller 1989)

Distance intervals (miles)	Maximum ^a dispersal distance	Final ^b dispersal distance	Total ^c dispersal distance
0 - 4.9	6	8	3
5 - 9.9	8	6	2
10 - 14.9	6	9	1
15 - 19.9	12	8	2
20 - 24.9	6	6	2
25 - 29.9	7	5	5
30 - 34.9	3	2	0
35 - 39.9	3	2	2
40 - 44.9	0	1	3
45 - 49.9	3	2	1
50+	2	1	5
Sample size	56	50	26
Mean	20.1	18.0	34.1
SD	14.0	13.3	26.3
CV	69.9%	74.0%	77.3%
Median	17.5	16.4	27.0
Percent >7 miles	80.4	76.0	76.9
Percent >12 miles	67.9	64.0	73.1
Percent >17 miles	53.6	44.0	69.2

^a Maximum distance is the greatest linear distance the juvenile traveled from the natal area.

^b Final distance is the linear distance from the natal area to the last point of detection.

^c Total distance is defined as the sum of all segments between successive location established as the bird dispersed from its natal area.

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Table P2—Dispersal distances of color-banded, juvenile spotted owls that survived at least 1 year

Source of data ^a	Sex	Year banded	Year resighted	Distance (miles)
Eugene District, BLM	F	1986	1987	7.5
Eugene District, BLM	M	1987	1988	16.0
Roseburg District, BLM	F	1986	1987	5.5
Roseburg District, BLM	U	1986	1987	18.0
Roseburg District, BLM	F	1986	1988	9.0
Roseburg District, BLM	M	1986	1988	7.8
Roseburg District, BLM	M	1986	1989	7.0
Roseburg District, BLM	M	1986	1989	5.0
Roseburg District, BLM	U	1986	1989	38.0
Roseburg District, BLM	M	1987	1988	4.3
Roseburg District, BLM	M	1987	1988	2.5
Roseburg District, BLM	M	1987	1989	7.5
Roseburg District, BLM	F	1988	1989	10.0
Medford District, BLM	M	1986	1987	6.0
Medford District, BLM	F	1988	1989	41.0
Salem District, BLM	M	1986	1988	1.7
Miller (pers. comm.)	F	1987	1989	9.7
Miller (pers. comm.)	M	1987	1989	5.0
Miller (pers. comm.)	M	1988	1989	9.2
Miller (pers. comm.)	F	1988	1989	19.0
				<i>n</i> = 20
				mean = 12.0
				SD = 10.7
				Median = 8.4

^a BLM data from files in District offices.

If juveniles carrying radio transmitters tend to die sooner than normal, we might expect our results to underestimate dispersal distance. Using the full data base, we found no significant difference in mean dispersal distances or number of days survived between the subset of birds ($n = 25$) that ceased dispersing at least 45 days before they died or their transmitters failed, and the subset ($n = 30$) for which information was lacking about when they ceased dispersing in relation to death or transmitter failure. To further test the hypothesis that transmitters had no effect on maximum dispersal distance, we computed a simple correlation. No relation between maximum dispersal distance and the period that birds wore transmitters ($r = -0.04$) was evident. We next subdivided the transmitter data into three groups (birds that carried radios from 1 to 150 days, 151 to 300 days, and >300 days), then computed means of the maximum linear distances these birds were recorded from their natal areas. Group means were 18.3 miles (SD = 13.0, $n = 29$), 23.7 miles (SD = 16.1, $n = 20$), and 20.9 miles (SD = 11.7; $n = 5$), respectively. No pair of means differed significantly (ANOVA—F-value = 0.846; $P > 0.43$; chi-square approximation by Kruskal-Wallis test— $X^2 = 1.52$; $P > 0.47$), again indicating that transmitters did not affect our estimates of dispersal distances. We have therefore used the full data set when estimating dispersal distances of radio-marked, juvenile spotted owls.

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Data from color-banded birds used to compile table P2 present a different problem. Because the area searched was constrained by field operation boundaries of the BLM in parts of Oregon where the birds were banded, no opportunity existed to re-locate birds that may have dispersed beyond those boundaries. We believe the estimate of mean dispersal distance from the banding data, therefore, underestimates the true mean by an unknown and potentially significant amount. The fact that the mean dispersal distance estimated from banded birds is lower than each of three estimates from radio-marked birds (table P1) is not surprising.

Appropriate Distance Between HCAs

Success of the spotted owl conservation strategy proposed here depends on frequent dispersal between HCAs, which means that HCAs must be separated by distances well within the known dispersal ranges of juveniles. We based our determination of appropriate distances between HCAs primarily on results from radio-marked birds (table P1), because we believe distances based on banded birds (table P2) underestimated true dispersal distances of juvenile spotted owls. We have not been able to determine a fully objective method to set a “safe” distance between HCAs, based on owl dispersal distances. That the distance need not include dispersal distances of 100% of the juveniles listed in table P1, however, seemed obvious. (One of those owls settled in its parents’ home range, giving it a final dispersal distance of 0 miles.) On the other hand, we believe the distances between HCAs should be well within the known dispersal distances of at least 50% of all juveniles. After lengthy discussions of this matter among all members of the Committee and advisors, and consultation with other authorities not closely affiliated with our efforts, we believe the distances between HCAs should be within the known dispersal distances of at least two-thirds (67%) of all juveniles. By setting the maximum allowable distance between the nearest points of contact of neighboring HCAs at 12 miles, we satisfy the 67% criterion for all three measures of dispersal distance in table P1. Visual comparison of the dispersal distances of radio-marked birds and distances between nearest neighbor HCAs (fig. P1) clearly shows that most HCAs are separated by distances well within the dispersal distances of juvenile spotted owls.

Birds that tended to disperse less than 12 miles would still have opportunities to join the floater population (see discussion in appendix O) in their natal HCA and eventually find vacancies in the breeding population there. Indeed, we contend that replacement of adults lost from the breeding population by recruits from within their natal HCA is the primary reason why larger blocks of habitat (hence more pairs of birds) tend to persist longer than smaller blocks with fewer pairs (appendices M and O). This opportunity would seldom be available in a fully developed network of SOHAs, however, because a bird that dispersed a relatively short distance would usually find itself in unsuitable habitat for breeding, and its natal area (the SOHA) would usually still be occupied by its parents. Birds dispersing from SOHAs would need to locate another SOHA to find suitable breeding habitat, and its availability would depend on whether the appropriate sex was missing from the pair in that SOHA.

Appendix P: Connectivity

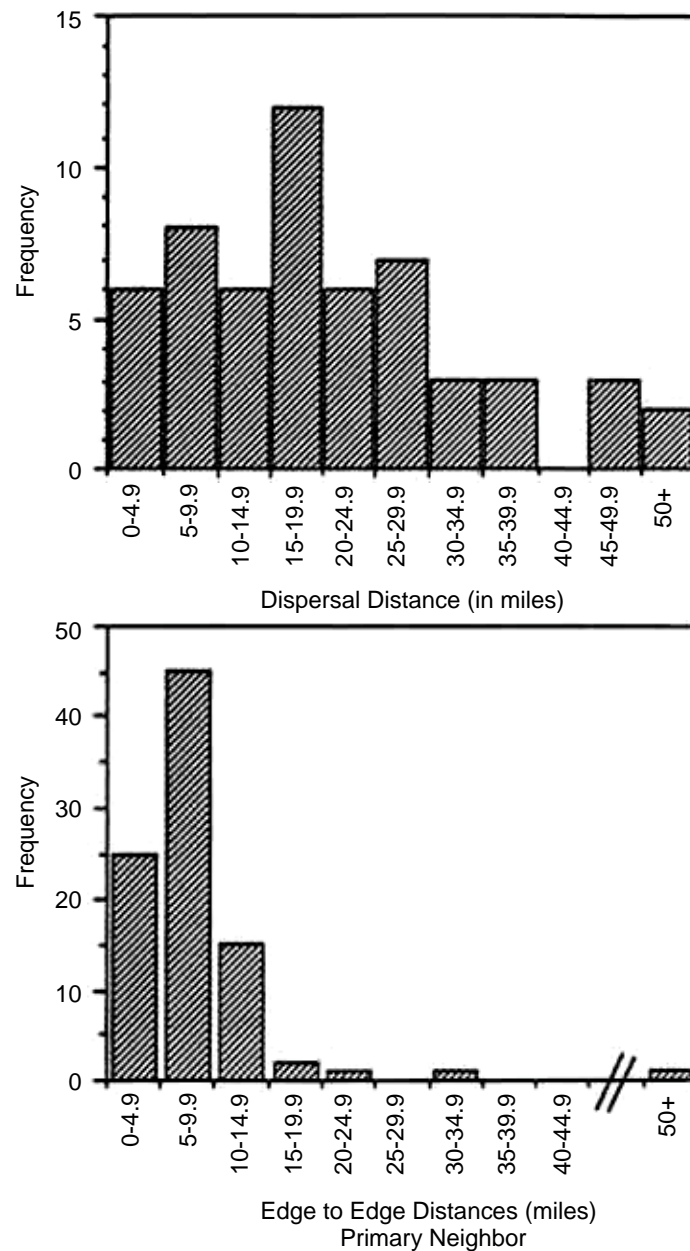


Figure P1—Comparison of maximum dispersal distances of radio-marked juveniles (upper histogram) and nearest distances between edges of neighboring HCAs (lower histogram).

Existing conditions in some locations precluded designation of HCAs with habitat adequate to support at least 20 pairs, either now or in the future. Some HCAs provide for even fewer than 10 pairs (see appendix Q). All else being equal, populations in these areas are likely to be more prone to local extinction than populations supported by larger areas. To provide an additional measure of security for small HCAs, we opted to increase the likelihood of successful dispersal from one to another by setting shorter distances between them (see appendix Q for specific guidelines). The distance selected, 7 miles, is less than the median distance estimated from banded birds (table P2) and is within the dispersal range of more than 75% of all radio-marked juveniles (table P1).

Appendix P: Connectivity

Connectivity

We use “connectivity” to mean the kinds and amounts of habitat occurring in the zones between HCAs. Conditions there must be compatible with the movement of spotted owls, such that they are both capable of moving through these habitats and inclined to do so. Although connecting zones need not assure habitat capable of supporting a pair of breeding owls, they do need to provide stopover places where owls can find suitable cover and, especially, foraging opportunities. To that extent, then, we believe that the connecting zones between HCAs must include some forested landscapes.

Guidelines for Habitat Conditions in Connecting Zones Between HCAs

We prefer to call areas of the forest matrix between HCAs the “connecting zones,” because we do not envision them as discrete corridors as implied in much recent literature (review in Wiens 1989). Available data do not allow formulation of specific corridor attributes for spotted owls, such as habitat features or configuration. Wiens (1989:217) cogently argues that “A focus exclusively on fragmentation of habitats misses the point that it is often the structure of an entire landscape mosaic rather than the size or shape of individual patches that is important to birds. The likelihood that dispersal can occur between fragments and forestall the extinction of sensitive species on a regional scale is influenced by the configuration of the fragments and the landscape mosaic in which they are embedded.” Elsewhere, Wiens (1989:227) again emphasizes the importance of the landscape context of habitat patches, pointing out that “To establish reserves according to ecological insights requires both a consideration of broad-scale landscape configurations and knowledge of the ecological requirements of the species that are important in particular situations.” This is the context within which we have formulated our recommendations on connectivity to assure the dispersal of owls between HCAs.

Studies indicate that juvenile spotted owls move freely through the landscape surrounding suitable habitat; hence, we believe they would generally ignore corridors designed especially to facilitate their dispersal between HCAs. Finally, we are concerned by speculation that relatively wide, linear strips of habitat suitable for spotted owls are likely to become havens for predatory species like great horned owls. Therefore, we have not planned for discrete corridors, but instead have developed management standards for the intervening matrix in the connecting zones between HCAs.

We prefer an option in which a major portion of the landscape in the connecting zones is potential dispersal habitat for owls, because we believe that a well-managed landscape matrix surrounding HCAs would facilitate dispersal among them while reducing the potential disadvantages of true corridors. These zones are not designated for preservation. Many existing management practices, including those associated with certain timber harvest methods, provide habitat attributes conducive to spotted owl dispersal. Examples include visual corridors, riparian corridors, and streamside-management zones, which contain possible stopover spots. These habitat areas tend to be linear in configuration. Additional forested patches that can serve for dispersal remain unharvested for other reasons. Forests on lands incapable of commercial timber production, on soils prone to slumping, and in special management areas for pileated woodpeckers and pine martens are examples of potentially suitable dispersal habitat for spotted owls. Furthermore, 50% of the landbase in a regulated forest would be older than 40 years, even with a rotation schedule of only 80 years. We expect much of that managed landbase to be suitable for passage by dispersing spotted owls (appendix R recommends studies to evaluate this expectation).

Appendix P: Connectivity

Standards and guidelines in this conservation strategy also specify that at least 50% of the forest matrix outside HCAs be maintained in stands of timber with a mean d.b.h. of 11 inches or greater, with at least 40% canopy closure. They also specify the retention of at least 80 acres of suitable owl habitat within a 1/4-mile of the nest tree or center of the presumed nest stand of all known pairs, up to seven per township, that are not included in other HCAs (see appendix Q). Although we believe these patches occasionally will be used by dispersing spotted owls, their primary value should be as nuclei of older forest, surviving from the current stand, that will become core areas for breeding pairs of spotted owls in the future, as the surrounding forest matrix grows up around them. We have seen numerous examples of this phenomenon throughout the range of the northern spotted owl. Old-growth patches in younger stands result from fires that left unburned segments of forest scattered here and there. Severe windstorms, and even inefficient logging practices in past years, have produced similar patchiness.

To explore the effectiveness of these guidelines for connectivity, we have mapped in detail the connecting zones between HCAs to show the distribution of stream corridors, forest stands by rotation age, forest patches reserved for a variety of other reasons, and the patches of forest that will be retained as HCA's around known pairs' activity centers (see figures P2, P3). We carefully chose connecting zones that represent the range of conditions on Federal land today. One zone is from the Mount Hood National Forest in Oregon (fig. P2), and the other is from the Gifford Pinchot National Forest in Washington (fig. P3). Maps of these zones are included as, a part of the documentation of this conservation strategy.

We believe standards developed here will provide for juvenile dispersal at rates sufficiently high to assure effective demographic interaction among HCAs. We also recognize that many dispersing juveniles will perish because they disperse in the wrong direction, starve to death for lack of experience in capturing prey, or fail to predators. But high mortality rates are the rule among juvenile birds, for these and other reasons. It is normal and should be expected.

Appendix P: Connectivity

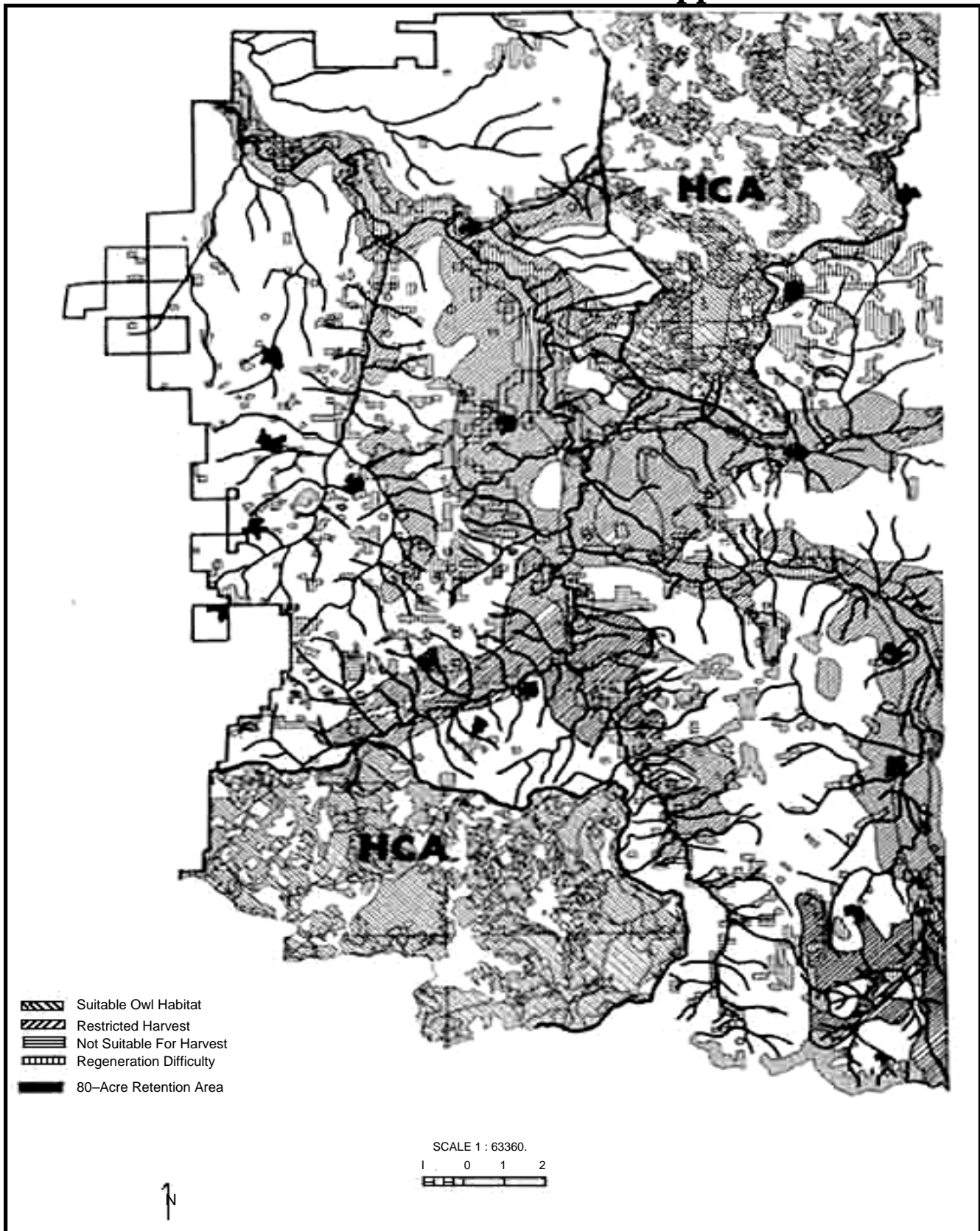


Figure P2—Land allocations in the Mount Hood National Forest Land-use Plan that demonstrate connectivity among HCM to facilitate dispersal.

Appendix P: Connectivity

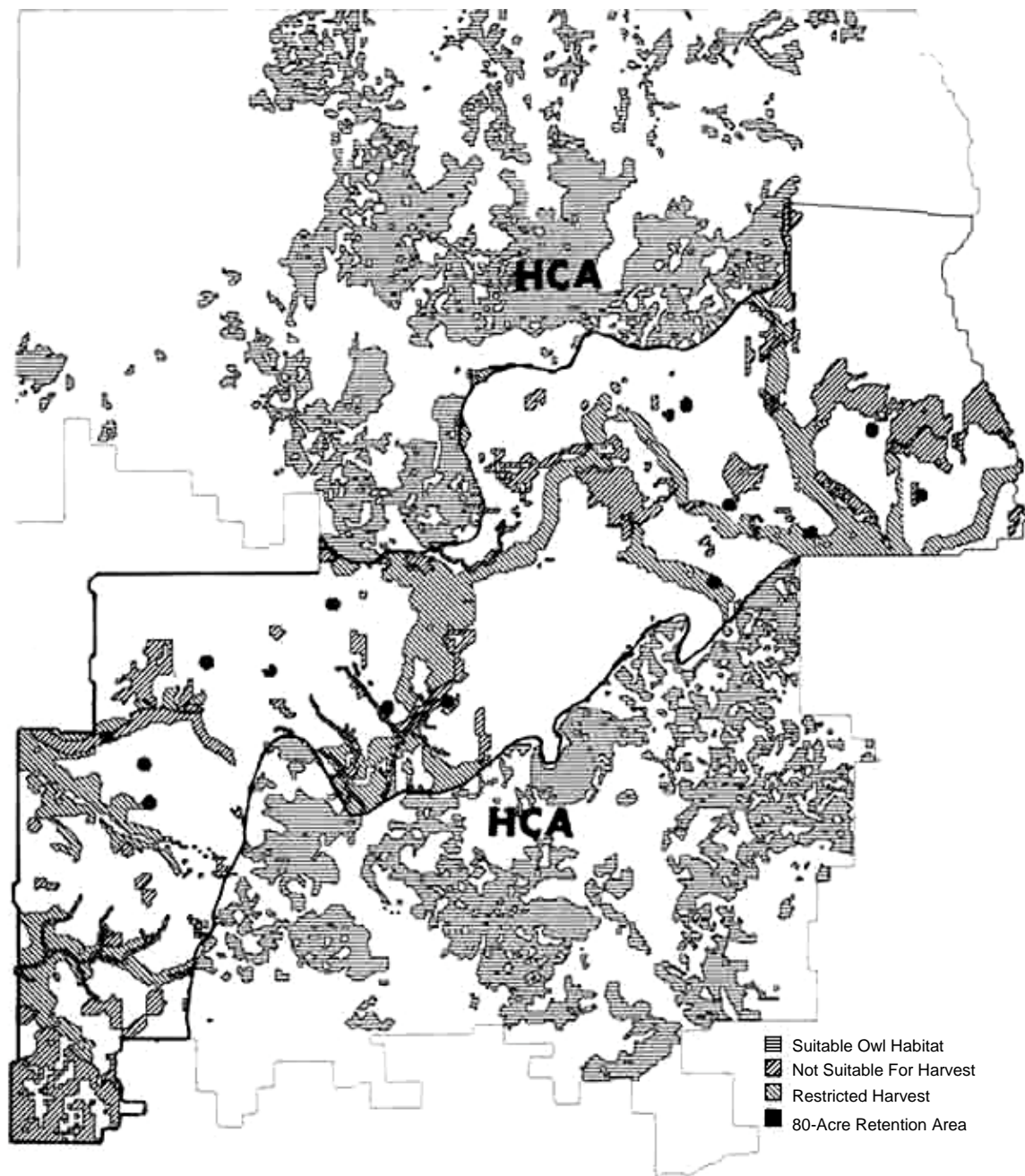


Figure P3—Land allocations in the Gifford Pinchot National Forest Land-use Plan that demonstrate connectivity among HCAs to facilitate dispersal.

Appendix P: Connectivity

References

- Diamond, J. M. 1975.** The island dilemma: Lessons of modern biogeographic studies for the design of natural reserves. *Biol. Conserv.* 7:129-146.
- Forsman, E. D. 1980.** Habitat utilization by spotted owls in the west-central Cascades of Oregon. Ph.D. Thesis, Oreg. State Univ., Corvallis. 95pp.
- Gilpin, M. E., and J. M. Diamond. 1976.** Calculation of immigration and extinction curves from the species-area-distance relation. *Proc. Natl. Acad. Sci. USA* 73:4130-4134.
- Gutiérrez, R. J. Pers. comm.** Humboldt State Univ., Arcata, Calif.
- Gutiérrez, R. J., J. P. Ward, A. B. Franklin, W. LaHaye, and V. Meretsky. 1985 unpubl.** Dispersal ecology of juvenile northern spotted owls (*Strix occidentalis caurina*) in northwestern California. Final rep. on Coop. Agreement PNW-82-226, Portland, Oreg. 48pp.
- Harris, L. D. 1984.** The fragmented forest. University of Chicago Press, Chicago. 211pp.
- Laymon, S. A. 1988.** Ecology of the spotted owl in the central Sierra Nevada, California. Ph.D. Thesis. Univ. California, Berkeley. 257pp.
- Meslow, E. C., and G. S. Miller. 1986 unpubl.** Dispersal of juvenile northern spotted owls in the Pacific Northwest Douglas-fir region. Progr. rep. Oreg. Coop. Wildl. Res. Unit, Dep. Fisheries and Wildlife, Oreg. State Univ., Corvallis.
- Miller, G. S. 1989.** Dispersal of juvenile northern spotted owls in western Oregon. M.S. Thesis. Oregon State Univ., Corvallis. 139pp.
- Miller, G. S. Pers. comm.** Oreg. State Univ., Corvallis.
- Noss, R. F. 1987.** Corridors in real landscapes: A reply to Simberloff and Cox. *Conserv. Biol.* 1:159-164.
- Noss, R. F., and L. D. Harris. 1986.** Nodes, networks, and MUMs: Preserving diversity at all scales. *Environ. Manage.* 10:299-309.
- Simberloff, D., and J. Cox. 1987.** Consequences and costs of conservation corridors. *Conserv. Biol.* 1:63-71.
- Soulé, M. E., D. T. Bolger, A. C. Alberts, J. Wright, M. Sorice, and S. Hill. 1988.** Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. *Conserv. Biol.* 2:76-92.
- Soulé, M. E., and D. Simberloff. 1986.** What do genetics and ecology tell us about the design of nature reserves? *Biol. Conserv.* 35:19-40.

Appendix P: Connectivity

- Terborgh, J. 1975.** Faunal equilibria and the design of wildlife preserves. Pages 369-380 *in* Tropical ecological systems: Trends in terrestrial and aquatic (F. Golley and E. Medina, eds.). Springer-Verlag, New York.
- Wiens, J. A. 1989.** The ecology of bird communities. Vol. 2: Processes and variations. Cambridge Univ. Press, New York.
- Willis, E. O. 1974.** Populations and local extinctions of birds on Barro Colorado Island, Panama. *Ecol. Monogr.* 44:153-169.
- Wilson, E. O., and E. O. Willis. 1975.** Applied biogeography. Pages 522-534 *in* Ecology and evolution of communities (M. L. Cody and J. M. Diamond, eds.). Belknap Press of Harvard Univ. Cambridge, Mass.